Growth and physiology of *Eucalyptus nitens* in plantations following thinning

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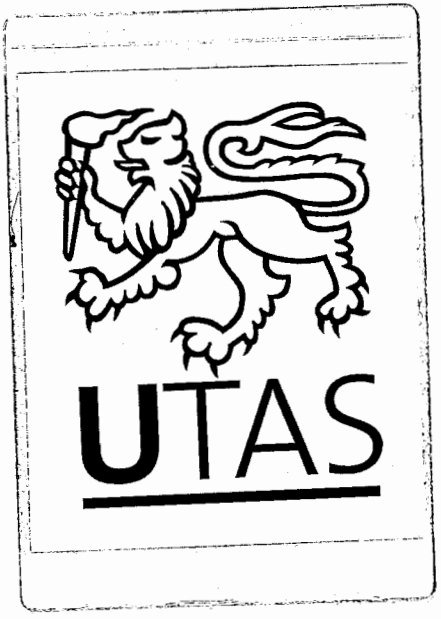
Declarations

This thesis contains no material which has been accepted for a degree or diploma by the University of Tasmania or any other institution. To the best of my knowledge and belief this thesis contains no material previously published or written by another person except where due acknowledgment is made in the text of the thesis.

Jane L. Medhurst



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Abstract

In Australia, a new activity is the management of eucalypt plantations for solid wood products. Thinning is one option for improving log sizes without the need for long rotation periods. The timing and intensity of thinning operations has a large bearing on the final products. This thesis describes a series of experiments in which the growth and physiological responses to thinning in *Eucalyptus nitens* (Deane and Maiden) Maiden plantations were identified. The thinning treatments, in three plantations, included an unthinned control and a range of final stockings from 600 to 100 trees per hectare.

Diameter growth was significantly improved by thinning. In general, the more trees removed by thinning, the higher the growth response by the retained trees. Dominant and co-dominant trees showed the greatest growth response to thinning. Plantations of low to medium productivity will benefit from early-age thinning. Based on stand and individual tree responses, a final density of 200 to 300 trees per hectare may be ideal.

The hydraulic conductivity of sapwood increased with stem height and the ratio of leaf area to stem sapwood area increased with stem size. Thinning did not alter these relationships. A broader study across a wide range of *E. nitens* plantations found strong relationships between stem sapwood area and tree leaf area that were independent of site, age and silvicultural treatment.

Crown structure and the development of stand leaf area index following thinning were investigated. Larger branches were found in the lower crown of thinned trees and the increase in leaf area as a result of thinning occurred on the northern aspect of the crown. For trees in unthinned stands, the vertical distribution of leaf area

was skewed towards the top of the crown and was correlated with live crown ratio. The vertical leaf area distribution of trees in a thinned stand was less skewed and was unrelated to tree size or dominance. Leaf area index, as estimated from light interception measurements, increased at a constant rate soon after thinning regardless of residual stand density. In the longer term, residual stand density had a strong influence on leaf area increase per tree and was correlated with changes in crown length.

Water use of retained trees increased after thinning through changes in the radial variation in sap flow across the sapwood. Stand-level water use after thinning was reasonably predicted from the Penman-Monteith equation scaled by a simple canopy size factor.

Increases in photosynthetic capacity and changes in foliar nitrogen distribution occurred after thinning. These responses were well correlated with measured changes in the light regime and were due primarily to changes in specific leaf area. Foliar nitrogen content was positively related to light levels throughout the crowns of trees in thinned and unthinned stands.

Thinning induced both short- and long-term physiological changes. A modelling analysis demonstrated that increases in crown light interception and light-use efficiency drive growth response. The relationship of these changes with environmental factors suggests that, in order to maximise individual tree and stand productivity, thinning regimes for *E. nitens* plantations should be designed to maintain adequate light levels for individual crowns between thinning and harvest.

Acknowledgments

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The cooperation of the Bass and Huon District staff of Forestry Tasmania in establishing the Lisle and Creekton thinning trials is gratefully acknowledged. The Lisle and Creekton trials were each thinned by skilled and obliging contractors. I thank Lance Pearce of Mechanised Logging and Frank Frankcombe of Aprin for their efforts.

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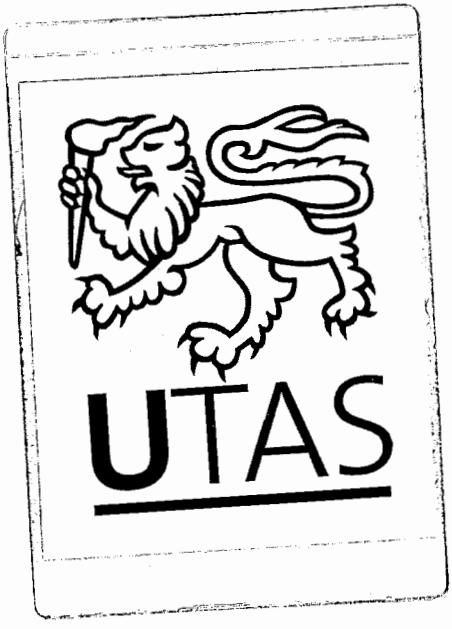
Lastly, but most importantly, I thank Peter McLoughlin. His love, support and encouragement made this thesis possible.



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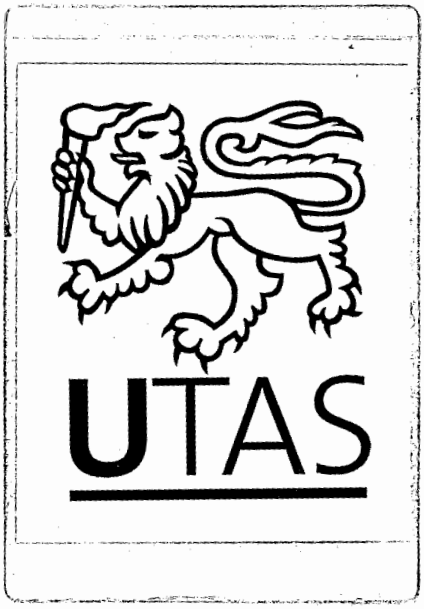


Chapter 1. Introduction

1.1 The issue

In Australia, native *Eucalyptus* forests have traditionally supplied the bulk of the sawlog resource. However, public disquiet in the past 20 years over logging practices and subsequent government inquiries has resulted in large tracts of forested land being placed into conservation and preservation areas. As a result, in 1990 approximately 20 per cent of the total native forest area was available for managed wood production and of this, only 15 per cent was considered to be of high production potential (Florence et al. 1990). As the native forest area available for wood production has declined, interest has grown in the potential of hardwood sawlog plantations to offset these resource losses.

Hardwood plantations represent a small, yet rapidly expanding proportion of the total plantation estate in Australia. In 1995, there were 158 000 hectares (ha) of eucalypt plantations in Australia which represented 15 per cent of the total plantation resource (ABARE 1998). In Tasmania there has been a significant increase in the hardwood plantation estate over the last 10 years. In 1995 there were 62 000 ha of eucalypt plantations in Tasmania, 39 per cent of the total eucalypt plantation estate in Australia (ABARE 1998). Between 1991 and 1996 over 6 000 ha of eucalypt plantations were established on public land in Tasmania under the federally-funded Intensive Forest Management Program (Farmer and Smith 1997). *E. nitens* was the main species planted, the product emphasis being on high quality appearance-grade timber and veneer. The knot-free timber required for such products relies on either natural branch-shed or mechanical

pruning. A plantation stocking of 1300 trees ha^{-1} does not provide adequate branch suppression and produces a large knotty core (Neilsen and Wilkinson 1990). Conversely, stockings below 1000 trees ha^{-1} produce large branches which carry a large pruning-associated decay risk (Neilsen and Gerrand 1999). Consequently, initial stockings of 1100 trees ha^{-1} are used for *E. nitens* plantations in Tasmania (Forestry Tasmania 1999). Given this initial stocking rate, a thinning regime is required if sawlog-sized trees are to be grown within a reasonable timeframe.

The rapid early growth rate of *E. nitens* succeeds in reducing the rotation length of plantations but makes the timing of a thinning to maximise growth of selected trees critical. In South Africa *E. nitens* has been classified as a very shade-intolerant species (Schönau and Coetzee 1989) and in Tasmania, Beadle and Turnbull (1992) found that peak current annual increment (CAI) of a *E. nitens* plantation established at 2400 trees ha^{-1} occurred at age five years, soon after canopy closure. Ideally a thinning regime in *E. nitens* plantations should prevent the final crop trees from experiencing intra-specific competition and enable growth of these trees to be maximised over the entire rotation. In reality, delaying the thinning until a commercial operation can be carried out is often required for the financial viability of the plantations (Gerrand et al. 1993; Forestry Tasmania 1999). The thinning regime used in the *E. nitens* plantations may ultimately need to reflect a compromise between optimising the growth rate of final crop trees and improving the financial performance of the plantations. In adopting this compromise however, it is assumed that *E. nitens* will still respond to thinning after a number of years of inter-specific competition. This study examines the physiological responses to thinning to establish how much flexibility exists for the

timing and intensity of thinning in *E. nitens* plantations.

1.2 Background

A number of studies of growth response to thinning in *Eucalyptus* plantations has established a positive growth response when thinning is carried out at an early age. The characteristic rapid early growth rate of *Eucalyptus* species from the *Symphyomyrtus* subgenus (Beadle and Inions 1990) may be extended if thinning is carried out before the onset of inter-specific competition. When thinning is delayed beyond this point, the capacity of trees to respond may be reduced. Thinning a productive *Eucalyptus globulus* Labill. plantation at age 11 years produced no growth response in the retained trees by age 13 years (Gerrand et al. 1997a). Thinning a *E. regnans* plantation at age 11.8 years had produced no growth response more than seven years after thinning (McKenzie and Hawke 1999). The reason for the lack of response may have been the poor tree health (McKenzie and Hawke 1999). Thinning in older natural stands of *Eucalyptus obliqua* L'Hérit (50 years old) resulted in a slower, more muted response compared with thinning an equivalent stand at 24 years of age: this was attributed to age-related decline in rates of crown and root expansion (Brown 1997). The impact on growth response to delayed thinning in *E. nitens* plantations has not been addressed to date.

1.3 The species

E. nitens is a fast-growing species with a natural distribution on the slopes of the Great Dividing Range from New South Wales to Victoria. The species belongs to the family *Myrtaceae* and has smooth bark, which is green when juvenile and grey on adult trees. It typically forms pure stands of tall open forest with trees of good

form and mature heights commonly in the range of 40 -70 m (Boland et al. 1984). In its natural range *E. nitens* is found at altitudes ranging from 600 to 1600 m and on sites with evenly-distributed annual rainfall ranging from 750 to 1750 mm (Boland et al. 1984). A feature of *E. nitens* is its ability to tolerate cold climates and frequent frosts (Pederick 1979; Raymond et al. 1992). This frost tolerance, combined with fast early growth rates and a light-coloured, straight-grained wood make *E. nitens* a ideal choice for sawlog plantations in Tasmania.

1.4 The current thinning prescription

The current prescription for thinning *E. nitens* plantations aims to maintain the rapid early growth of the selected final crop trees. On good quality sites, where dominant and co-dominant trees may eventually out-compete the pruned final crop trees, the stand is released by thinning from 1100 trees ha^{-1} to approximately 1000 trees ha^{-1} at age 3 or 4 years. The stand is then commercially thinned between ages 7 to 12 years when the stand is reduced to a final stocking of 300 trees ha^{-1}. The final crop trees are then harvested at age 25 years (Forestry Tasmania 1999). Delaying the second thinning until a commercial thinning can be imposed aims to maximise the financial return from the plantation. On low quality sites, where thinning volumes are unlikely to be commercially viable, thinning is done earlier and to waste. To date, silvicultural research on thinning in eucalypt plantations has focused on the response to early, waste thinning (Gerrand et al. 1997b). Early thinning protects trees from intra-specific competition and, if it is intense enough, maintains optimal growth rates of individual trees. Within-row canopy closure in these fast-growing *E. nitens* plantations usually occurs at age 2 or 3 years (Smethurst 1998) and full canopy closure can be expected soon after. Therefore a later-age thinning releases trees from intra-specific competition. Little

research exists which addresses the potential of intra-specific competition to significantly depress the growth of individual trees and reduce their ability to respond to later-age thinning.

1.5 Objectives

This study addresses a number of objectives, namely;

- to establish patterns of height and diameter growth of *E. nitens* for different size classes following thinning
- to provide a detailed description of the impact of thinning on canopy development and crown activity
- to measure the duration of thinning response and relate this to time of thinning and canopy activity

1.6 Summary of each chapter

Chapter 1. Introduction

A general introduction to the study.

Chapter 2. General materials and methods

This chapter describes the study sites used in the study. The research is described in the following six chapters.

Chapter 3. Growth in response to early-age and later-age thinning

This chapter outlines and compares the growth response of *E. nitens* following a waste-thinning at age 6 years in one plantation, and following a commercial pulpwood thinning at ages 8 and 9 years in two plantations. This chapter has been accepted for publication as;

Medhurst, J.L., Beadle, C.L. and Neilsen, W.A. (*in press*) Later-age and early-age thinning affects growth, dominance and intra-specific competition in *Eucalyptus nitens* plantations. *Canadian Journal of Forest Research.*

Chapter 4. Leaf area - sapwood area relationships and sapwood hydraulic conductivity in thinned and unthinned *E. nitens* trees

The relationship of tree leaf area to stem sapwood area is determined for thinned and unthinned trees. This chapter tests the hypotheses that; (i) thinned stands of *E. nitens* will have a greater slope of the relationship between sapwood area and leaf area, and (ii) any increase in the sapwood area - leaf area relationship will be reflected in a proportional increase in hydraulic conductivity of sapwood.

Chapter 5. Allometric relationships for *E. nitens*

Allometric relationships from the preceding chapter are more fully explored. Additional data from Cherry et al. (1998), White et al. (1998) and Hunt (1999) is included to examine the generality of allometric relationships in *E. nitens*. This chapter has been published as;

Medhurst, J.L., Battaglia, M., Cherry, M.L., Hunt, M.A., White, D.A. and Beadle, C.L. (1999) Allometric relationships for *Eucalyptus nitens* (Deane and Maiden) Maiden plantations. *Trees* 14: 91-101.

Chapter 6. Changes in crown structure and stand leaf area index

This chapter examines the effect of stand density on the crown structure of *E. nitens*. The objectives were to (i) characterise the crown structure and vertical distribution of leaf area for mid-rotation (10 to 15 year-old) *E. nitens* plantations, (ii) determine the effect of thinning on crown structure and vertical distribution of leaf area and (iii) quantify the rate of recovery of canopy leaf area following

thinning. This chapter has been accepted for publication as;

Medhurst, J.L. and Beadle, C.L. (*in press*) Crown structure and leaf area index development in thinned and unthinned *Eucalyptus nitens* plantations. *Tree Physiology*.

Chapter 7. Water use in thinned *E. nitens* stands immediately after thinning

This chapter examines changes in the pattern of water use of trees and stands soon after thinning. The Penman-Monteith model is adapted to enable predictions of stand water use following thinning to a range of final stand densities. This study tested the hypothesis that following thinning, water use of retained *E. nitens* trees was proportionally higher than trees in the unthinned stand.

Chapter 8. Impact of thinning on crown processes and crown environment

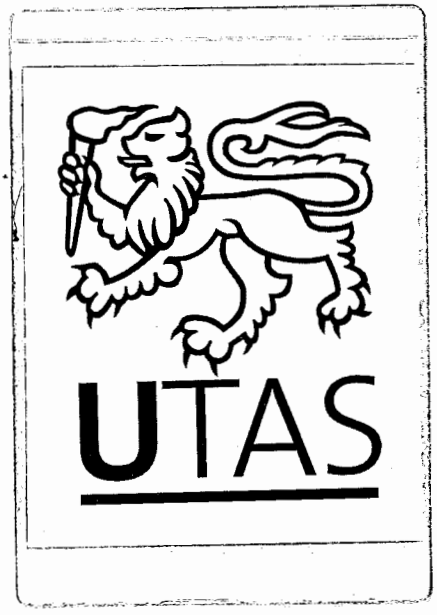
This chapter details the changes in photosynthetic rates, light environment and foliar nutrient levels following thinning. The objectives of the study were to (i) determine the extent to which maximum photosynthetic rates (A_{max}) of *E. nitens* are affected by thinning treatment, (ii) relate the spatial pattern of A_{max} within the crown to the changes in light environment caused by thinning, and (iii) establish if the responses of A_{max} to thinning are driven by changes in foliar nitrogen or phosphorus concentrations.

Chapter 9. The physiological basis for thinning *E. nitens*: a modelling analysis

This chapter describes an exercise undertaken to examine the importance of physiological responses to thinning in terms of their impact on tree and stand growth. A simple light-use efficiency model was used for the analysis.

Chapter 10. A discussion of management implications

This chapter draws the major findings of this study together and explores their implications for management of *E. nitens* sawlog plantations.



Chapter 2. Description of thinning trials

2.1 The plantations

Three trials were used in the study of thinning response in *E. nitens* plantations. These plantations are referred to as the Lisle, Creekton and Goulds Country plantations in this thesis. All three plantations were owned by Forestry Tasmania. The locations of the trials are shown in Figure 2.1.

The Lisle thinning trial was situated at an altitude of 220 m above sea level (asl). The ex-native forest site had fine sandy clay loam over clay gradational soils formed on Silurian-Devonian sandstone and siltstone. The topsoil depth ranged from 20 to 70 cm. The site was logged in 1987, burnt and windrowed but no cultivation was carried out prior to planting. Pre-planting herbicide application was carried out two months prior to planting. The actual *E. nitens* provenance is unknown but is likely to be from native forest seed collected from the Toorongo provenance (Forestry Tasmania, pers. comm.). Planting in 1987 was at 3.0 x 2.4 m (1389 trees ha^{-1}) spacing. No fertilizer was applied to this plantation. The closest meteorological station (Australian Bureau of Meteorology) was located at Scottsdale, 15 km from the plantation and at an elevation of 190 m asl. The long-term mean annual rainfall was 1038 mm with a winter peak and an average of 155 rain days per year (days a^{-1}) (Figure 2.2). The mean daily maximum temperature was 17.2 °C and the mean daily minimum temperature was 6.9 °C. On average there were 19 days a^{-1} where the minimum temperature was less than 0 °C.

Figure 2.1 Map of Tasmania showing the location of the the Creekton, Lisle and Goulds Country thinning trials.

The Creekton thinning trial was located at an altitude of 120 m asl. The ex-native forest site had red-brown gradational soils formed on Jurassic dolerite. The 1914 regrowth *E. obliqua* was clearfelled prior to 1989 (Turnbull et al. 1992). The trial site was burnt, windrowed using a bulldozer and rip-mounded. Pre-planting herbicide application was carried out six weeks before planting. This consisted of an aerial application of 6 kg ha^{-1} active ingredient (a.i.) of atrazine and 2 kg ha^{-1} a.i. amitrole plus 2 kg ha^{-1} a.i. ammonium thiocyanate. Prior to planting, triplesuperphosphate (120 kg ha^{-1} of elemental phosphorus) was applied to the trial site. Planting in 1989 was at 3.5 x 2.0 m (1430 trees ha^{-1}) spacing. The actual *E. nitens* provenance is unknown but originates from native forest seed collected from the western distribution of *E. nitens* in Victoria. A meteorological station (CSIRO) was located within the Creekton plantation, approximately 500 m from the thinning trial. The Creekton plantation received 1086 mm rainfall a^{-1} (Figure 2.3). The mean weekly maximum temperature was 19.5 °C and the mean weekly minimum temperature was 3.3 °C.

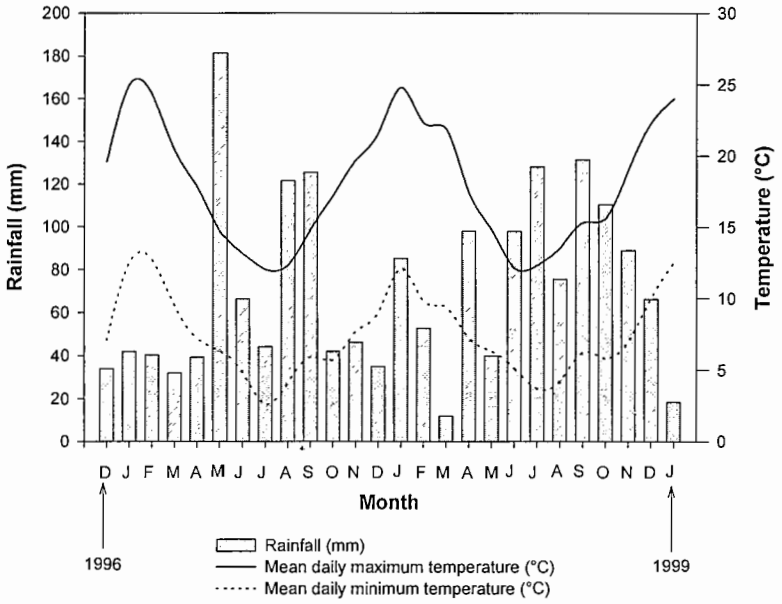


Figure 2.2 Monthly rainfall and monthly averages of daily maximum and minimum temperatures at Scottsdale, near the Lisle thinning trial, December 1996 to January 1999.

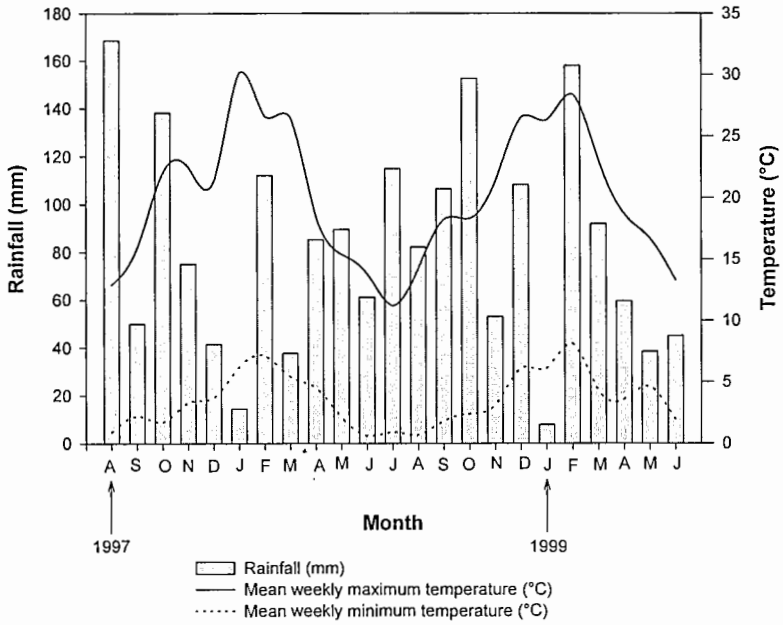


Figure 2.3 Monthly rainfall and mean weekly maximum and minimum temperatures at Creekton, August 1997 to March 1999.

The Goulds Country thinning trial was located at an altitude of 120 m asl. The site previously carried *E. regnans* native forest. The soils were classified as yellow podsolic soils formed on adamellite granites. The area was logged, burnt and windrowed but no cultivation or chemical weed control was carried out prior to planting. Toorongo provenance *E. nitens* was planted in 1984 at 3.5 x 2.5 m (1143 trees ha^{-1}). No cultivation or control of the woody weeds was carried out. The nearest meteorological station (Australian Bureau of Meteorology) was located at St. Helens at 5 m asl where conditions were likely to be warmer and drier than those experienced at the plantation site. Mean annual rainfall at St. Helens was

776 mm (Figure 2.4). Mean daily maximum temperature at St. Helens was 18.4 °C and mean daily minimum temperature was 7.4 °C. A mean annual rainfall of 1000 mm was estimated for the Goulds Country site (Gerrand et al. 1997a).

Site and stand characteristics of the three plantations are summarised in Table 2.1.

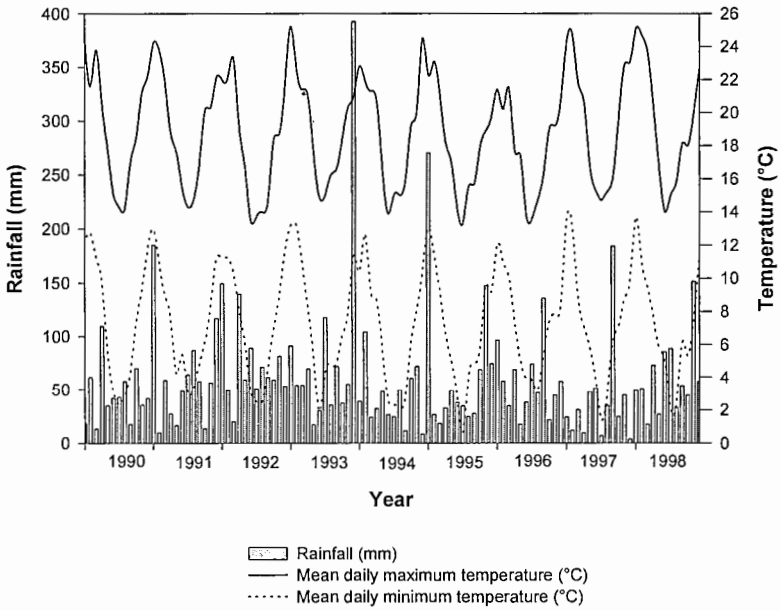


Figure 2.4 Monthly rainfall and monthly averages of daily maximum and minimum temperatures at St. Helens, near Goulds Country, 1990 to 1998 inclusive. Note the record monthly rainfall of 392 mm during December 1993.

Table 2.1 Summary statistics for the Goulds Country, Lisle and Creekton *E. nitens* plantations showing measures of tree variables immediately prior to thinning.

	Goulds Country	Lisle	Creekton
Grid reference	41°05' S 148°06' E	41°13' S 147°22' E	43°21' S 146°54' E
Mean annual rainfall (mm)	776[a]	1055	1086
Mean daily max. temperature (°C)	18.4[a]	17.2	19.5[b]
Mean daily min. temperature (°C)	7.4[a]	6.8	3.3[b]
Altitude (m; ASL)	120	220	110
Age (years)	6	9	8
Stems per hectare	999	1031	1256
Mean height (m)	11.2	20.2	16.6
Mean diameter (cm)	11.9	18.5	14.5
Diameter range (cm)	0.5 - 25.7	2.7 - 35.2	0.4 - 27.8
Mean annual increment at age 9 years (m^3 ha^{-1} a^{-1})[c]	10.1	26.2	19.8

[a]Meteorological data from St. Helens weather station near sea level, 27 km from thinning trial site.
[b]Mean maximum or minimum weekly temperature.
[c]For unthinned stand

2.2 Trial design and treatments

At the Lisle plantation, three replicates of four thinning treatments were assigned in a randomised block design to plots of 15 x 55 m (0.08 ha). The thinning treatments were 100, 250, 600 trees ha^{-1} and an unthinned control. The trial was thinned as part of a commercial mechanised thinning operation during December 1996 and January 1997. Third row outrows were used in each plot, with further removal of trees in the remaining rows to the designated density. A buffer of one outrow plus one retained row was used along the rows in each plot. Across the rows of each plot, a minimum buffer of 5 m was used.

The Creekton trial was identical to the Lisle trial in terms of treatments and trial

design. Plot layout differed between the two trials because of location of wind rows. The Creekton trial had plot dimensions of 30 x 25 m (0.08 ha). The trial was thinned using a feller-buncher as part of a commercial mechanised thinning operation during August 1997. Wind damage occurred in the low density plots due to a strong wind event two months after thinning. An average of 19 per cent of stand basal area was lost from the 100 trees ha^{-1} treatment as a result of wind damage. An average of 10 per cent of stand basal area was lost from the 250 trees ha^{-1} treatment.

The Goulds Country *E. nitens* thinning trial was established in 1990 by Forestry Tamania (then Tasmanian Forestry Commission) as part of a research project to determine appropriate thinning and pruning regimes for sawlog production from *E. nitens* plantations in Tasmania. This trial investigated the response to a high intensity, early aged thinning. Five levels of treatment were applied in a randomised block design with four replicates. The treatments were 100, 200, 300 and 400 trees ha^{-1} and an unthinned control. Plot size was 25 x 40 m (0.1 ha). Plots were thinned to waste using chainsaws. A pruning treatment was overlaid with two replicates pruned to 6 m and two replicates unpruned for each of the thinning treatments. A buffer row surrounding each plot was treated with the same thinning and pruning treatments. The growth response from ages six to ten years of age has been reported for this trial (Gerrand et al. 1997b).

Chapter 3. Growth, dominance and intra-specific competition after early- and later-age thinning

3.1 Introduction

Achieving the required diameter of crop trees in the shortest time possible is a commonly held goal of managers of sawlog plantations (Fry 1983; Koistinen 1985; Neilsen and Wilkinson 1990; Kerr 1996; Gerrand et al. 1997b). Progressive thinning regimes, where the stand is reduced to its final density in a number of stages, have been tested. Two thinnings were recommended for eucalypt plantations of initial density greater than 1000 trees ha^{-1} in New Zealand (Deadman and Hay 1987). Fry (1983) also recommended a two-stage thinning for *Eucalyptus saligna* Smith and *E. regnans* plantations in New Zealand. A recommended thinning regime for *Eucalyptus grandis* W. Hill ex Maiden plantations in South Africa reduces the density from 1333 trees ha^{-1} to 250 trees ha^{-1} over four thinnings (Schönau and Coetzee 1989). Initially multi-stage thinning regimes were considered expensive to implement on an industrial scale in Australia and direct regimes, where a single early-age, non-commercial thinning is used to bring the stand from initial to final density, were preferred (Neilsen and Wilkinson 1990). However, financial analyses of silvicultural regimes for sawlog plantations in Tasmania have shown a later-age commercial thinning regime to offer the best return on good quality sites with a site index over 25 m (mean dominant height at age 15 years) (Gerrand et al. 1993; Candy and Gerrand 1997).

The current prescription for thinning *E. nitens* plantations aims to maintain the

rapid early growth of the selected final crop trees. As dominant and co-dominant trees may eventually out-compete the final crop trees, the stand is release-thinned from 1100 trees ha^{-1} to approximately 1000 trees ha^{-1} at age 3 or 4 years. The stand is then commercially thinned between ages 7 to 12 years when the stand is reduced to a final density of 300 trees ha^{-1}. The final crop trees are then harvested at age 20 to 25 years (Forestry Tasmania 1999). Delaying the second thinning until a commercial thinning can be carried out is done to maximise the financial return from the plantation.

Silvicultural research on thinning in *E. nitens* plantations had focused on the response to early-age non-commercial thinning (Gerrand et al. 1997b). Early thinning protects trees from intra-specific competition and, if it is intense enough, maintains optimal growth rates of individual trees. Within-row canopy closure in fast-growing *E. nitens* plantations usually occurs at age 2 or 3 years (Smethurst 1998) and full canopy closure can be expected soon after. Therefore a later-age thinning releases trees from intra-specific competition. An understanding of the effect of intra-specific competition on the growth of individual trees and how this reduces their subsequent response to later-age thinning is needed for designing sound thinning regimes.

The main objective of this study was to quantify the height and diameter growth of *E. nitens* trees and stands after thinning at different stages of development. The stand density used at planting was reduced to a range of final densities. A plantation which had recently reached full canopy closure (early-age thinning) and two plantations which had experienced full canopy closure for at least two years (later-age thinning) were used.

3.2 Materials and Methods

3.2.1 Sites and treatments

This experiment used the Goulds Country, Lisle and Creekton thinning trials, which are described in Chapter 2. The thinning treatments at each trial are described in Table 3.1 in terms of thinning intensity.

Table 3.1 Thinning intensity described in terms of density and basal area reduction at the three *E. nitens* thinning trials, Goulds Country age 6 years, Creekton age 8 years and Lisle age 9 years.

Treatment	Pre-thin		Post-thin		% reduction	
	trees ha^{-1}	BA (m^2 ha^{-1})	trees ha^{-1}	BA (m^2 ha^{-1})	trees ha^{-1}	BA (m^2 ha^{-1})
Goulds Country						
100 trees ha^{-1}	993	11.7	100	2.4	89.9	79.3
200 trees ha^{-1}	1033	10.8	200	4.2	80.6	60.7
300 trees ha^{-1}	1028	11.4	300	6.3	70.8	45.2
400 trees ha^{-1}	1053	10.7	400	7.6	62.0	29.1
unthinned	890	11.0	890	11.0	0.0	0.0
Lisle						
100 trees ha^{-1}	1063	30.6	100	4.1	90.6	86.6
250 trees ha^{-1}	967	29.9	250	9.6	74.1	67.9
600 trees ha^{-1}	1058	31.0	596	20.9	43.7	32.6
unthinned	1038	28.9	1038	28.9	0.0	0.0
Creekton						
100 trees ha^{-1}	1320	26.8	100	3.4	92.4	87.3
250 trees ha^{-1}	1150	20.3	250	6.9	78.3	66.0
600 trees ha^{-1}	1300	23.8	600	14.7	53.8	38.2
unthinned	1254	22.6	1250	23.2	0.0	0.0

3.2.2 Measurements

3.2.2.a Early-age thinning trial

A canopy dominance class was assigned to each tree prior to thinning. Diameter over bark at breast height (1.3 m) of each tree was measured annually.

Total tree height was measured annually for seven years on a sample of trees in each plot at a rate of 100 trees ha^{-1}. Green crown height (point of junction between

branch and stem for lowest green branch) was measured in 1997 only. Heights were measured using a digital hypsometer ('Vertex', Forestor Instruments AB, Sweden). Half of the height trees in each plot at Goulds Country were the tallest trees, to enable an estimate of mean dominant height, while the remaining half were randomly selected trees.

The best 100, 200, 300 and 400 trees ha^{-1} were identified in each of the twenty plots at establishment of the thinning treatment. This was done by ranking trees based on stem size and potential merchantability class. The potential merchantability class was derived from a form assessment which used a categorical system for branching, stem form, defects and damage (Table 3.2). This enabled statistical comparison of equal numbers of trees across all thinning treatments.

Table 3.2 Potential merchantability classification system used for ranking trees at each trial. (reproduced from Gerrand et al. 1997a).

Potential merchantability class	Description	Stem form	Stem scarring	Branch
1	Potential high quality sawlog	no visible lean, sweep, or kinks	Nil	Up to 3 branches over 35 mm diameter Branch angle ≤ 45°
2	Potential sawlog	lean < 8°, sweep < 10 cm, slight kinks	Slight scarring permitted (surface only, <½ circumference, <180 cm	Maximum of six branches over 35 mm Branch angle not limiting
3	Pulpwood	lean < 15°, sweep 10-20 cm, kink inside centreline	No damage limit except presence of charcoal	Less than 10 branches over 10 cm diameter
4	Unmerchantable	Poorer than above	No limit	No limit

3.2.2.b Later-age thinning trials

A canopy dominance class was assigned to each tree prior to thinning in both the Lisle and Creekton trials. Diameter over bark at breast height (1.3 m) of each tree was measured every six months for two years.

Total tree height and green crown height were measured on a sample of trees in each plot at a rate of 100 trees ha^{-1}. All height trees were randomly selected. Heights were measured using the digital hypsometer.

The best 100, 250, and 600 trees ha^{-1} were identified in each of the plots at establishment of the thinning treatment. As at Goulds Country, selection of these groups of trees was based on a criteria of tree size, form and spacing (Gerrand et al. 1997a).

3.2.3 Data analysis

Stand basal area was calculated by summing individual tree basal areas and expressed on a per hectare basis. For each trial, stand basal area increment across the entire measurement period was calculated by subtracting the standing basal area at time of thinning from that of the last growth measurement. Mean annual basal area increment of individual trees was also calculated across the entire measurement period by subtracting basal area at thinning from basal area at the last growth measurement. At Goulds Country, destructive sampling in the 200 trees ha^{-1} and control treatments occurred in the seventh year after thinning (see Chapters 4 and 5). Therefore, direct comparisons of stand basal area between treatments seven or more years after thinning were not valid.

Live crown ratio (LCR) was calculated as;

$$LCR = \frac{H_t - H_g}{H_t} \qquad 3.1$$

where H_t is total tree height and H_g is green crown height. Mean height, height increment and LCR were calculated for each plot.

The effect of thinning treatment on stand basal area increment, mean tree basal area increment, mean total height and mean LCR was assessed using analysis of variance in the GLM procedure of the SAS statistical analysis system (SAS Institute Incorporated 1990). The effect of pruning treatment on growth at Goulds Country was also investigated. Differences between mean treatment values were investigated using the least significant difference (LSD) test ($\alpha = 0.05$).

3.3 Results

3.3.1 Early-age thinning

3.3.1.a Stand basal area increment

Relative to the unthinned treatment, a reduction in stand basal area increment during the six years of measurement was found in the 100, 200 and 300 trees ha^{-1} treatments only ($p < 0.05$, Figure 3.1). The significant reduction in the 100 trees ha^{-1} treatment was observed in the first year after thinning and was sustained throughout the measurement period. The reduction in the 200 trees ha^{-1} treatment became apparent in the second year after thinning and was also sustained until the end of the measurement period. The reduction in the 300 trees ha^{-1} treatment occurred in the second and third years only. The proportion of basal area reduced was directly related to thinning intensity (Table 3.1). The cumulative basal area growth six years after thinning was 52%, 20% and 9% less than the unthinned

control for the 100, 200 and 300 trees ha^{-1} treatments respectively. The 400 trees ha^{-1} treatment maintained similar cumulative basal area increments to the unthinned control throughout the first six years after thinning (Figure 3.1).

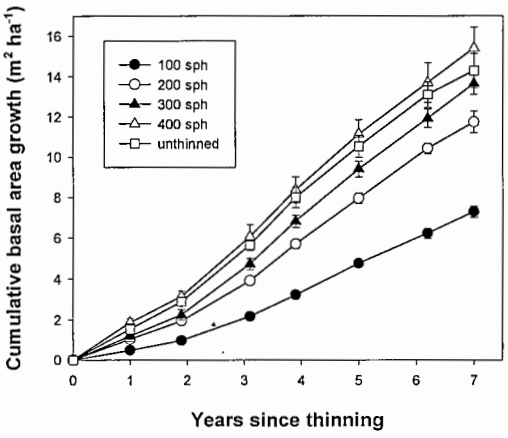


Figure 3.1 ***E. nitens*** **mean cumulative stand basal area increment (m^2 ha^{-1}) by thinning treatment measured for the seven years following thinning at Goulds Country. The cumulative basal area increment seven years after thinning in the 200 trees ha^{-1} and control treatments includes the basal area of a set of destructively sampled trees which were felled 6 months prior to this measurement. Error bars show mean standard errors.**

3.3.1.b Basal area increment of select groups of trees

A comparison of the cumulative basal area increment of equal numbers of trees across thinning treatments showed a strong and sustained response to thinning (Figure 3.2a-d). Six years after thinning, the cumulative basal area increments of the best 100, 200, 300 and 400 trees ha^{-1} in each thinning treatment were significantly higher than the growth of the equivalent number of trees in the unthinned control ($p < 0.05$, Figure 3.2a-d).

For the top 100 trees ha^{-1} in each treatment, a thinning response was observed in

the first year after treatment. By the third year after thinning, the basal area increment of the top 100 trees ha^{-1} in the 100 and 200 trees ha^{-1} treatments was significantly higher than in the remaining treatments ($p < 0.05$) and by the end of the fourth year, that of the top 100 trees ha^{-1} in the 300 and 400 trees ha^{-1} treatments was significantly higher than the unthinned control ($p < 0.05$, Figure 3.2a). There was no difference in growth of the top 100 trees ha^{-1} in the 100 and 200 trees ha^{-1} treatments throughout the measurement period. Six years after thinning, the mean stand basal area increment of the 100 trees ha^{-1} treatment was 127% higher than that of the best 100 trees ha^{-1} in the unthinned control.

For the top 200 trees ha^{-1}, a significantly greater basal area increment was observed in the 200 trees ha^{-1} treatment in the first year after thinning ($p < 0.05$) but in the 300 and 400 trees ha^{-1} treatments not until the fourth year after thinning. The trees in the 200 trees ha^{-1} treatment maintained a higher basal area increment than all other treatments throughout most of the measurement period (Figure 3.2b). Six years after thinning the mean stand basal area increment of the 200 trees ha^{-1} treatment was 90% greater than that of the best 200 trees ha^{-1} in the unthinned control.

For the top 300 trees ha^{-1}, a significantly greater basal area increment was observed in the 300 and 400 trees ha^{-1} treatments in the fourth year after thinning ($p < 0.05$, Figure 3.2c). The cumulative basal area increment of the top 400 trees ha^{-1} was significantly higher than that in the unthinned control in the second year after thinning ($p < 0.05$). While there was no significant difference between the treatments in the third year, the basal area increment of the 400 trees ha^{-1} treatment was again higher in the fourth year ($p < 0.05$). This higher basal area increment was sustained for the rest of the measurement period (Figure 3.2d).

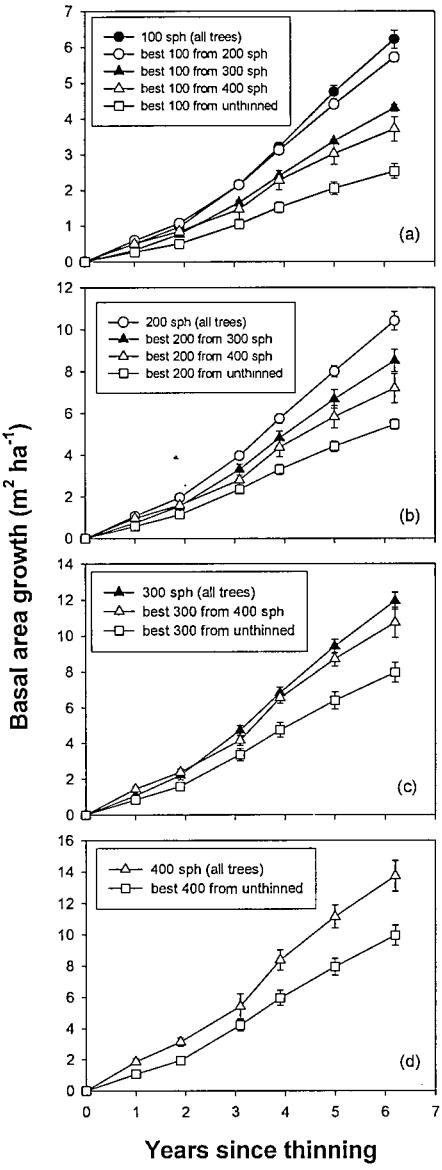


Figure 3.2. ***E. nitens*** **mean cumulative basal area growth (m^2 ha^{-1}) for select groups of trees by thinning treatment at Goulds Country. (a) top 100 trees ha^{-1} (b) top 200 trees ha^{-1} (c) top 300 trees ha^{-1} and (d) top 400 trees ha^{-1}. Error bars show mean standard errors.**

Pruning treatment did not interact with thinning treatment and did not affect growth (Table 3.3).

Table 3.3 Results from analysis of variance of the basal area increment of the best 100 trees ha^{-1} at Goulds Country *E. nitens* trial, one year after treatment.

	Df	Sum of Sq	Mean Sq	F value	Pr(F)
Thin	4	0.2849	0.0712	5.0915	0.0201
Prune	1	0.0031	0.0031	0.2242	0.6471
Block	1	0.0693	0.0693	4.9508	0.0531
Thin:Prune	4	0.0671	0.0168	1.1984	0.3753
Residuals	9	0.1259	0.0140		

3.3.1.c Basal area growth by initial dominance class

Dominance class at the time of thinning affected the degree of growth response of individual trees. Thinning had a highly significant effect on the growth of dominant trees ($p < 0.01$). The degree of response was directly related to thinning intensity (Figure 3.3). In the six years after thinning, the dominant trees in the 100 trees ha^{-1} treatment grew on average 706 cm^2 in basal area at breast height. This was 108% greater than the growth of the dominant trees in the unthinned control. Co-dominant trees exhibited a similar response to thinning ($p < 0.01$). Again, the magnitude of the response was directly proportional to the intensity of the thinning (Figure 3.3). Sub-dominant trees did not respond to thinning ($p > 0.05$).

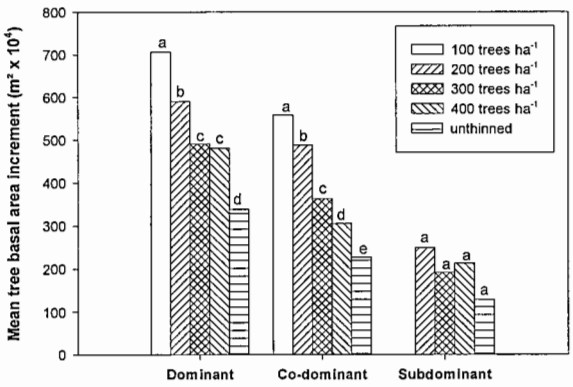


Figure 3.3. *E. nitens* mean tree basal area increment ($m^2 \times 10^4$) from 1990 to 1997 by thinning treatment and dominance class, Goulds Country. Letters in each dominance class indicate homogeneous groupings of thinning treatments (LSD $\alpha = 0.05$).

3.3.1.d Height growth

Height growth was unaffected by thinning seven years after thinning ($p > 0.05$, Table 3.4). However, mean live crown ratio (LCR) showed a significant response to thinning ($p < 0.05$). Mean LCR was 0.53 in the unthinned control compared to 0.66 in the 100 trees ha^{-1} treatment seven years after thinning (Table 3.4).

Table 3.4 *E. nitens* live crown ratio (LCR) at age 14 years and mean height increment from age 6 to 14 years by thinning treatment at Goulds Country. Least Significance Difference (LSD) homogeneous groupings are identified by letters ($\alpha = 0.05$).

Thinning treatment	Mean LCR	Mean height increment (m)
100 trees ha^{-1}	0.66 a	9.9 a
200 trees ha^{-1}	0.60 b	10.6 a
300 trees ha^{-1}	0.59 bc	10.0 a
400 trees ha^{-1}	0.55 bc	10.7 a
control (unthinned)	0.53 c	8.5 a

3.3.2 Later-age thinning

3.3.2.a Stand basal area increment

A significant reduction in the stand basal area increment of the 100 and 250 trees ha^{-1} treatments relative to the unthinned treatment was measured six months after thinning at both Lisle and Creekton ($p < 0.05$, Figure 3.4a,b). At Creekton this lower level of stand growth was maintained throughout the measurement period. However, the basal area increment of the 250 trees ha^{-1} treatment at Lisle recovered and was similar to that of the unthinned control 12 months after thinning. After 18 months, the stand basal area growth of the 600 trees ha^{-1} treatment at Lisle was significantly higher than the unthinned control ($p < 0.05$). After two years, the basal area growth of the 600 trees ha^{-1} treatment (8.88 m^2 ha^{-1}) was 28% greater than the unthinned control (6.92 m^2 ha^{-1}).

After two years the cumulative basal area increments of the 100 and 250 trees ha^{-1} treatments at Creekton were 80% and 57% lower, respectively, than in the unthinned control. At Lisle, the cumulative basal area growth of the 100 trees ha^{-1} treatment was 55% less than the unthinned control after the same period of time.

3.3.2.b Basal area increment of select groups of trees

At Lisle, a growth response of the top 100 trees ha^{-1} was measured in all treatments in the first six months after thinning and this was sustained throughout the measurement period ($p < 0.05$, Figure 3.4c). After 12 months, the basal area increments of the top 100 trees ha^{-1} in the 100 and 250 trees ha^{-1} treatments were significantly higher than in the 600 trees ha^{-1} treatment ($p < 0.05$). After two years, the cumulative basal area increments of the top 100 trees ha^{-1} in the 100, 250 and 600 trees ha^{-1} treatments were, respectively, 135%, 157% and 84% higher

than that of the best 100 trees ha^{-1} in the unthinned control. For the top 250 trees ha^{-1}, the basal area increments measured in the 250 and 600 trees ha^{-1} treatments in the first six months after thinning were significantly higher than that of the unthinned treatment ($p < 0.05$, Figure 3.4e). This was maintained throughout the measurement period. After 18 months, the basal area increment in the 250 trees ha^{-1} treatment exceeded that of the top 250 trees ha^{-1} in the 600 trees ha^{-1} treatment ($p < 0.05$). After two years, the basal area increments of these trees in the 250 and 600 trees ha^{-1} treatments were both significantly higher ($p < 0.05$) than the increment of the best 250 trees ha^{-1} in the unthinned control (116% and 74% respectively). For the top 600 trees ha^{-1}, a significantly higher basal area growth was observed in the 600 trees ha^{-1} treatment than in the unthinned control throughout the measurement period ($p < 0.05$, Figure 3.4g).

At Creekton there was no significant thinning response in the basal area growth of the top 100, 250 and 600 trees ha^{-1} across treatments throughout the measurement period ($p > 0.05$, Figure 3.4d, f and h). The growth response in the first 12 months after thinning was erratic (eg. Figure 3.4d). The growth response in the 12 to 24 months after thinning was of a pattern similar to Lisle and Goulds Country. The trend was for the basal area growth to increase with the thinning intensity in each of the best 100, 250 and 600 trees ha^{-1} groups. However this response was not significant ($p > 0.05$).

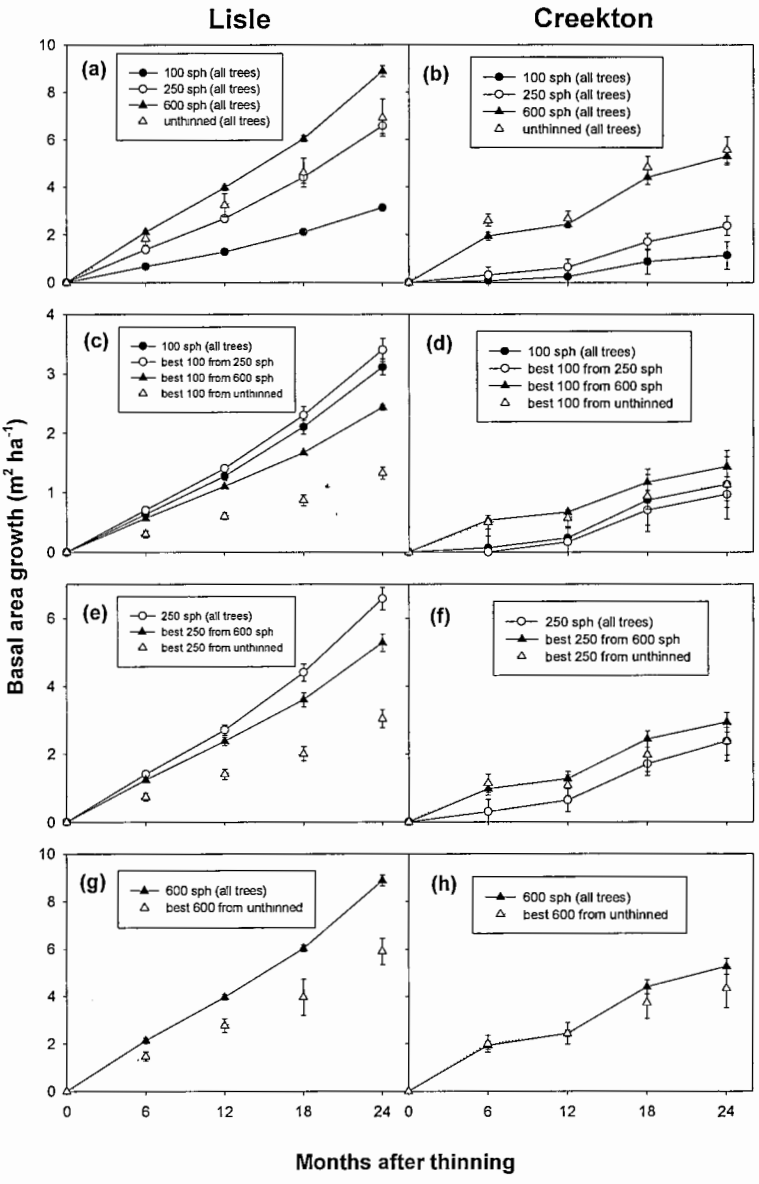


Figure 3.4 ***E. nitens*** **mean cumulative basal area growth (m^2 ha^{-1}) for select groups of trees by thinning treatment at Lisle: (a) all trees, (c) top 100 trees ha^{-1}, (e) top 250 trees ha^{-1} and (g) top 600 trees ha^{-1} and Creekton: (b) all trees, (d) top 100 trees ha^{-1}, (f) top 250 trees ha^{-1} and (h) top 600 trees ha^{-1} for the two years after thinning. Error bars show mean standard errors. Note that different y-axis scales are used for each select group of trees.**

3.3.2.c *Basal area growth by initial dominance class*

At Lisle, there was a significant response to thinning by dominant and co-dominant trees in the 100 and 250 trees ha^{-1} treatments ($p < 0.05$). In the 100, 250 and 600 trees ha^{-1} treatments, the mean basal area increment of dominant trees was, respectively, 120%, 99% and 21% greater than the unthinned dominants, two years after thinning (Table 3.5).

Table 3.5 *E. nitens* mean cumulative basal area increment by tree dominance class two years after thinning at Lisle and Creekton. Least Significance Difference (LSD) homogeneous groupings are identified by letters ($\alpha = 0{,}05$).

Thinning treatment	Dominant trees (cm^2)		Co-dominant trees (cm^2)		Sub-dominant trees (cm^2)	
Lisle						
100 trees ha^{-1}	334.9	a	216.1	a	-	-
250 trees ha^{-1}	303.2	ab	170.1	b	64.6	a
600 trees ha^{-1}	184.3	bc	105.2	c	6.2	b
control (unthinned)	152.1	c	68.3	d	8.8	b
Creekton						
100 trees ha^{-1}	276.2	a	184.9	a	113.2	a
250 trees ha^{-1}	205.6	ab	139.0	b	83.5	a
600 trees ha^{-1}	175.9	b	100.3	c	51.3	b
control (unthinned)	154.0	b	61.7	d	14.8	c

Co-dominant trees in all thinned treatments also responded strongly to thinning ($p < 0.01$). The magnitude of the response was directly related to thinning intensity. The mean co-dominant tree basal area increments in the 100, 250 and 600 trees ha^{-1} treatments were, respectively, 216%, 149% and 54% greater than that of unthinned co-dominants, two years after thinning (Table 3.5).

Sub-dominant trees in the 250 trees ha^{-1} treatment at Lisle responded to thinning (Table 3.5). Sub-dominant trees retained in the 600 trees ha^{-1} treatment did not respond to thinning. No sub-dominant trees were retained in the 100 trees ha^{-1}

treatment.

There was also a significant response to thinning by dominance class at Creekton. The mean basal area increment of dominant trees two years after thinning was directly related to the intensity of thinning. However, a significant response was found in the 100 trees ha^{-1} treatment only ($p < 0.05$). In this heaviest thinning treatment, dominant trees grew on average 79% faster than unthinned dominant trees.

Co-dominant trees at Creekton responded strongly to thinning with the degree of response directly proportional to the intensity of thinning ($p < 0.05$). The mean basal area increment of co-dominant trees in all thinning treatments was significantly greater than unthinned co-dominant trees. The mean basal area increments of co-dominant trees in the 100, 250 and 600 trees ha^{-1} treatments were, respectively, 200%, 125% and 63% greater than the unthinned co-dominants two years after thinning. Sub-dominant trees at Creekton did show a significant response to thinning ($p < 0.05$, Table 3.5), despite their overall contribution being minimal. There was no significant difference between the basal area growth of subdominants in the 100 and 250 trees ha^{-1} treatments ($p > 0.05$).

The relative response to thinning was greatest in the sub-dominant class and least in the dominant class at both Lisle and Creekton (Table 3.5).

3.3.2.d Height growth

The mean height increment at Lisle in the two years after thinning was not significantly affected by thinning (Table 3.6). However, the mean LCR of unthinned trees became significantly lower ($p < 0.05$) than that of thinned trees during this period. The mean LCR of unthinned trees decreased from 0.50 at time

of thinning to 0.44 two years later. The mean LCR of all other thinning treatments increased during this period (Table 3.6).

Table 3.6 *E. nitens* mean live crown ratio (LCR) before and two years after thinning and mean height increment after thinning by thinning treatment at Lisle and Creekton. LSD homogeneous groupings are identified by letters ($\alpha = 0.05$).

Thinning treatment	Mean LCR at thinning	Mean LCR after thinning	Mean height increment after thinning (m)
Lisle			
100 trees ha^{-1}	0.54 a	0.55 a	3.1 a
250 trees ha^{-1}	0.54 a	0.59 a	2.6 a
600 trees ha^{-1}	0.51 a	0.53 a	2.9 a
control (unthinned)	0.50 a	0.44 b	3.3 a
Creekton			
100 trees ha^{-1}	0.60 a	0.55 ab	2.5 a
250 trees ha^{-1}	0.64 a	0.58 a	3.0 a
600 trees ha^{-1}	0.56 a	0.50 ab	2.6 a
control (unthinned)	0.54 a	0.48 b	2.0 a

Mean height increment at Creekton was not significantly affected by thinning ($p > 0.05$, Table 3.6). The mean LCR of all treatments had decreased two years after thinning.

3.4 Discussion

3.4.1 Changes in basal area

In this study a growth response to high intensity thinning was found in *E. nitens* plantation trees after both early- and later-age thinning operations. A direct comparison of early-age thinning versus later-age thinning is difficult because of differences between the sites used in the study. However, the findings suggest that a growth response to later-age thinning can be achieved in highly productive plantations.

There was little stand basal area growth in the 100 and 250 trees ha^{-1} treatments at the Creekton site in the 12 months after thinning. This reduced growth was attributed to wind damage sustained in these plots from a strong wind event two months after thinning. An average of 19 per cent and 10 per cent of stand basal area was lost from the 100 trees ha^{-1} and 250 trees ha^{-1} treatments, respectively, as a result of wind damage. Wind damage is a potential risk when thinning is delayed as initial density used for eucalypt plantations in Tasmania will eventually restrict tree diameter growth but will generally not reduce height growth (Gerrand et al. 1997b). Guidelines exist for some species for timing thinning in order to minimise risk of wind damage (eg. Pinus radiata D. Don Cremer et al. 1982). Under these guidelines the height to diameter ratio at time of thinning at Lisle and Creekton placed both sites in a high risk category for stem failure. However no wind damage was found at Lisle after a strong wind event approximately one year after thinning and all of the wind damage at Creekton was in the form of root uplifting, with no trees suffering stem failure. The assessment of wind risk when thinning eucalypt plantations less than 10 years old should therefore be a local assessment, using knowledge of the soil characteristics and the susceptibility of the site to strong winds.

At both early- and later-age thinning trials, the growth responses to thinning became apparent soon after thinning and were sustained throughout the duration of the experiments. The rate of appearance of a thinning response varies between species. In an eight-year-old *Pinus taeda* L. stand, the growth response emerged two years after thinning (Ginn et al. 1991) and seven years after thinning in a 21-year-old *Quercus petraea* (Mattuschka) Liebl. and *Quercus robur* L. stand (Kerr 1996). The rapid response in *E. nitens* is consistent with that of a fast-growing

species. The particularly rapid response to thinning at Lisle was indicative of a high degree of competition prior to thinning. As Lisle was the more productive of the two later-age thinning sites, results from this study suggest that site quality determines the growth response after later-age thinning.

High intensity thinning means that site resources will be initially under-utilised by the stand. Improved growth rates and yield of individual trees offset the loss in stand production. Yet very high intensity thinning can produce a stand which is unable to regain the full use of site resources during the rotation. In *P. radiata* stands, a final density of 200 trees ha^{-1} was found to have a growth pattern that maintained a considerably lower stand basal area with time relative to both unthinned and less intensively thinned treatments (Whyte and Woollons 1990). While stand basal area growth declined with increasing thinning intensity at each of the sites in the present study, it was only the 100 trees ha^{-1} treatments that showed a distinctly lower basal area growth trajectory with time. This indicates that *E. nitens* at this density is unlikely to fully utilise the site during the rotation.

The effect on growth of lower densities was apparent from the experiments at Goulds Country and Lisle. When comparing similar numbers of trees across treatments, the greater the thinning intensity, the higher the growth response. The lower growth response at higher densities can be attributed to higher levels of intra-specific competition. It indicates that a fast-growing species such as *E. nitens* can benefit from high intensity thinning and thus maximise individual tree growth if competition remains absent for a reasonable length of time.

Response of the best 100 trees ha^{-1} in the 200 or 250 trees ha^{-1} treatment was similar to that of the 100 trees ha^{-1} treatment at Goulds Country and Lisle in the first two years after thinning. This indicated that, at least in the short term, little

growth advantage is achieved by thinning to a density as low as 100 trees ha^{-1}. However, the basal area (and hence diameter) growth of the 100 trees ha^{-1} treatment at the Goulds Country trial was beginning to exceed that of the best 100 trees ha^{-1} in the 200 trees ha^{-1} treatment in the sixth year after thinning. By the end of the rotation the differences in diameter between the two treatments could be quite large. This study has shown a positive correlation between thinning intensity and individual tree growth response. However, the final density is ultimately an economic decision where the extra value from larger individual tree sizes at lower densities must be weighed against the significantly lower stand basal area growth at these lower densities.

Across all three trials the removal of less than 50 per cent of basal area by thinning did not significantly reduce the total basal area increment of the stand. Removing up to 50 per cent of total stand basal area did not reduce the gross basal area increment in a number of thinning studies in native eucalypt forest (Webb and Incoll 1969; Goodwin 1990; Brown 1997). The '50 per cent rule' does not appear to be confined solely to *Eucalyptus* species. Thinning to 85, 75 and 60 per cent of stand basal area at age 35 years in a *Picea abies* (L.) Karst. stand did not reduce stand basal area increment in the 17 years after thinning (Koistinen 1985). The '50 per cent rule' could be used as a guide in release-thinning of *E. nitens* plantations early in the rotation.

The higher stand basal area growth in the 600 trees ha^{-1} treatment at Lisle when compared with the unthinned treatment suggests that the stand was experiencing intense competition at time of thinning that resulted in a less-than-maximum stand basal area growth. At Creekton, thinning to 600 trees ha^{-1} resulted in a 10 per cent decrease in basal area increment, while a 30 per cent increase in basal area growth

was observed at Lisle after a similar reduction in basal area. This contrasting response between the two later-age thinning trials may be due to differences in age, and stand size at thinning. The unthinned trees at the older and more productive Lisle stand were possibly experiencing greater competitive pressure than unthinned trees at the Creekton site. Thus on high quality sites, the basal area of a lightly thinned stand may rapidly converge on the basal area of the unthinned stand. It is unlikely that the basal area of the thinned stand would exceed the basal area of the unthinned stand as the thinned stand would eventually experience similarly high levels of competition. A convergence in basal area after thinning was also found in high quality *E. regnans* forest (Brown 1997) and high quality *P. taeda* stands (Hasenauer et al. 1997).

3.4.2 Dominance class

Growth response to thinning was proportional to dominance class, with the greatest basal area growth increment occurring in the trees classed as dominant at time of thinning. In sub-dominant trees, the relative growth response to thinning was large, but their overall contribution to stand basal area growth was small. In other species, temporal variation has been found in the thinning growth response of different tree size classes. For example, suppressed *Pinus sylvestris* L. trees initially showed a high relative growth response to thinning, yet after five years had the lowest relative and absolute growth response (Pukkala et al. 1998). Hence the selection of sub-dominant *E. nitens* trees for the final crop is not recommended. In native eucalypt forest it has been suggested that dominant trees, being relatively free of competition, will not respond to thinning unless other dominant trees are removed (Webb 1966). This argument was not supported by Brown (1997) who found that the magnitude of the thinning response was

proportional to the dominance class of the tree in *E. obliqua* and *E. regnans* native forest. This study has also found that dominant trees will respond to thinning. However, thinning was carried out early in the rotation of these plantations. In young plantations, differences between tree sizes are less pronounced than in mature stands. Hence the largest trees retained could still have benefited from the release of competition. Thinning in these plantations should aim to retain the most dominant trees of good stem form to maximise individual tree growth response.

3.4.3 Height growth

This study found that height growth in *E. nitens* was insensitive to thinning at all thinning intensities. Similar findings have been reported for *E. regnans* (McKenzie and Hawke 1999) and *E. grandis* (Schönau 1984). This contrasts with other studies which have reported height responses for *E. saligna* (Williamson 1979) and *E. regnans* (Messina 1992). In these studies, dominant, taller trees show reduced height increment after thinning while the less dominant trees show an increase in height increment. The lack of height response in the present study may be due to the random height sampling undertaken at each trial which meant that mean dominant height across thinning treatments was not directly measured. However, the insensitivity of height to thinning treatment may be due to patterns of biomass allocation and the relative strengths of 'source-sink' relationships within each tree. Apical tissues act as strong sinks for carbohydrates due to their proximity to the foliage producing the carbohydrates (Lanner 1985) and the competitive advantage gained by the tree from occupying a larger space (Smith 1986). If height growth has a high priority in biomass allocation it is expected that it will be insensitive to stand density.

The decline in the live crown ratio of unthinned *E. nitens* trees with age is likely

to result in a slowing of growth. The live crown ratio approximates the ratio of photosynthetic to non-photosynthetic (ie. respiring) surface area and is an index of the ability of the crown to nourish the remainder of the tree (Smith 1986). The lack of height growth response to thinning meant that observed changes in mean live crown ratios was caused by thinned trees retaining foliage in the lower sections of the crown, thus retaining or improving general vigour. Both the increase, and a slower decline, in mean live crown ratio with thinning found in this study have been reported for other tree species (Ginn et al. 1991; Peterson et al. 1997). The improved light conditions and photosynthetic performance of the lower crown after thinning (Ginn et al. 1991; Tang et al. 1999) is likely to prolong the retention of the lower crown.

3.4.4 Thinning intensity

A recommendation of a final stand density between 200 and 300 trees ha^{-1} can be made from careful consideration of the data. A final stand density of 100 trees ha^{-1} was characterised by large individual tree growth yet low stand basal area (Figures 3.1, 3.4a and b). Such a stand is seriously under-utilizing the site resources. It can be reasonably argued that, for a 25-year rotation, thinning to such a low density is unwarranted and similarly sized trees can be produced with a higher stand density. In terms of an upper limit for final stand density, this study showed that while individual tree growth was improved with low stand densities (Figures 3.2a,b and 3.4c,e), stand basal area growth was not compromised by densities as low as 250 trees ha^{-1} (Figures 3.1 and 3.4a). Stand densities above the recommended upper limit for final stand density are likely to be sacrificing individual tree growth, without gaining extra stand growth.

Growth response to later-age thinning was found in an *E. nitens* plantations which

was less than ten years old and had a mean annual increment of 26.2 m^3 ha^{-1} a^{-1} (Table 2.1) at time of thinning. A growth response to early-age thinning was also found. This suggests that some growth opportunity for final crop trees is lost as a result of delaying thinning past the age where canopy closure occurs. However, findings from this study suggest that the age at thinning during the first 10 years of the rotation in eucalypt plantations on highly productive sites may not be a crucial parameter in determining if trees will respond to thinning. Further research into the effect of site quality on growth response to later-age thinning is required if commercial thinning regimes are adopted for eucalypt plantation estates.

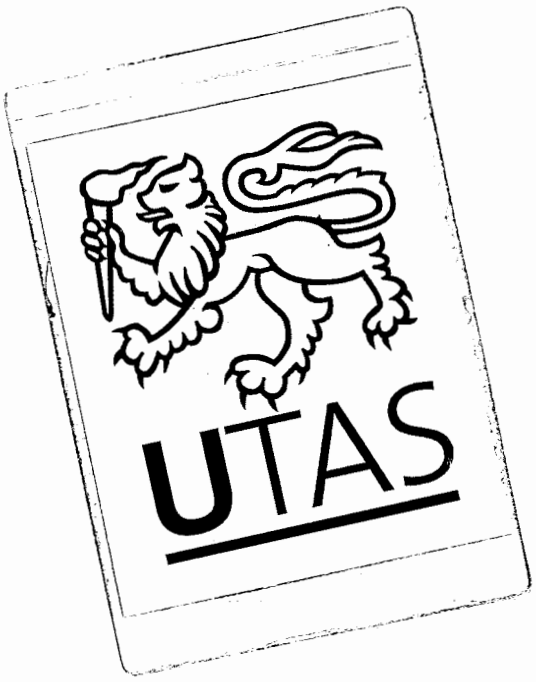
3.5 Conclusions

This experiment has demonstrated that *E. nitens* is able to respond strongly to thinning treatment. It is likely that a sub-optimal growth rate of individual trees occurs between the onset of full canopy closure and the time of thinning. However *E. nitens* on high quality sites has demonstrated a capacity to respond to delayed thinning.

The current thinning prescription for *E. nitens* plantations in Tasmania recommends a light release thinning to 1000 trees ha^{-1} at age 3 or 4 years and a commercial thinning to 300 trees ha^{-1} between the ages 7 to 12 years on high quality sites. The release thinning should reduce intra-specific competition and the commercial thinning is expected to produce a growth response in the final crop stand. Thinning to a final stocking of 200 to 300 trees ha^{-1} is expected to allow free growth of final crop trees throughout most of the rotation of 20 to 25 years without seriously under-utilising the site resources.

Growth responses to thinning may be due to adjustments in the relationship

between water supply (*ie.* stem sapwood) and water demand (*ie.* tree leaf area). This hypothesis is explored in Chapter 4.



Chapter 4. Leaf area – sapwood area relationships and sapwood hydraulic conductivity

4.1 Introduction

Reliable estimates of leaf area[1] are obtained using allometric relationships between structural components. Sapwood area can be an accurate scalar due to its role in supplying water to the transpiring foliage (Shinozaki et al. 1964a; b). Close relationships between leaf area and sapwood area have been demonstrated for a range of tree species (eg. Grier and Waring 1974; Waring et al. 1976; Rogers and Hinckley 1979; Kaufmann and Troendle 1981; Albrektson 1984; Espinosa-Bancalari et al. 1987; Coyea and Margolis 1992; Penner and Deblonde 1996; White 1996). The nature of the relationship for a given species may be influenced by site conditions (Espinosa-Bancalari et al. 1987; Shelburne et al. 1993; Mencuccini and Grace 1995; Berninger and Nikinmaa 1997), stand age (Albrektson 1984), and stand density (Shelburne et al. 1993).

Any change in the relationship between sapwood area and leaf area after thinning is a physiological response to restore the balance between water supply and use. Increases in the transpiration rate per unit leaf area after thinning (Morikawa et al. 1986) might be expected to lower the ratio between leaf area and sapwood area. However, increases in sapwood hydraulic conductivity would be expected to increase the ratio (Whitehead et al. 1984a). Increases in hydraulic conductivity with growth rate have been attributed to larger growth rings, and hence lower

[1] In all instances throughout this thesis, the term 'leaf area' refers to projected, or one-sided leaf area.

latewood proportion, in the sapwood (Booker and Kininmonth 1978; Edwards and Jarvis 1982; Whitehead et al. 1984a). In addition, any higher priority in allocating carbon to foliage after thinning (Mitchell et al. 1996) may increase the ratio (Shelburne et al. 1993).

This chapter describes an analysis of structural relationships using data from thinned and unthinned *E. nitens* plantations and tests the hypothesis that the amount of leaf area per unit sapwood area will be greater after thinning due to higher sapwood hydraulic conductivity. Estimates of leaf area are needed for a range of applications including growth modelling (Fownes and Harrington 1990), transpiration (Dye and Olbrich 1993), and light interception (Korzukhin and Ter-Mikaelian 1995). As such, an investigation into the effect of thinning on leaf area – sapwood area ratios is needed to provide a framework in which to consider other physiological responses to thinning.

4.2 Materials and methods

4.2.1 Field sampling

Sampling was undertaken at the Goulds Country thinning trial. Details of this trial can be found in Chapter 2. For the purpose of this study, sampling was restricted to the 200 trees ha^{-1} and control thinning treatments only.

Destructive sampling was carried out during winter 1997. To ensure sampling across the range of tree sizes, the diameter distribution at each site was divided into eight classes and a tree selected at random from each of the classes. Diameter distribution of the thinned stand at Goulds Country was based on four 0.1 ha plots (80 trees). Sampling in the unthinned stand was restricted to the best 200 stems ha^{-1} and the diameter distribution of these trees was determined from four 0.1 ha

plots (80 trees). Selection of the trees for destructive sampling had to consider the plantation owner's request that no more than two trees per plot were removed. In the thinned treatment, the 200 trees ha^{-1} were divided into four equal classes based on diameter. Two trees were randomly selected from each diameter class. To stratify the selection by plot firstly plot number was randomly selected, followed by diameter class. One tree from the selected plot and the selected diameter class was randomly selected. This process was repeated until two trees were selected from each of the 200 trees ha^{-1} plots.

The top 200 trees ha^{-1} in the unthinned control plots were identified when the trial was established in 1990. By limiting the tree selection to the top 200 trees ha^{-1}, the comparison between thinning treatments is based on trees which were of similar size and form prior to thinning. Random tree selection in the control plots was carried out using the same method described above. The characteristics of the sampled trees are described in Table 4.1.

Table 4.1 Summary statistics for destructively sampled trees at Goulds Country. Mean values are given with minimum and maximum values in parentheses.

Treatment	No.	Diameter at 1.3m (cm)	Height (m)	Green crown depth (m)
200 trees ha^{-1}	8	30.7 (23.4 - 38.7)	21.6 (20.6 - 24.6)	13.6 (12.3 - 15.4)
unthinned	8	25.6 (16.4 - 34.9)	19.2 (15.6 - 21.6)	10.9 (6.8 - 14.8)

For each tree, diameter at breast height (1.3 m) was measured. The tree was then felled and measured for total height and height to green crown base (point of emergence of lowest live branch). The green crown length was divided into three equal zones (lower, middle and upper). These crown zones were marked on the stem and stem diameters measured at these points.

For each zone, diameter of live branches was measured at 40 mm from the stem. Five branches which represented the range of branch diameters were selected from each zone. The five branches were excised at the stem junction, labelled and placed in plastic bags for transport to the laboratory. The branches were stored at 4 °C for a maximum of five days before processing.

To determine sapwood area, a 25 mm disc was cut from the stem from a height of 1.3 m, and from the base of the green crown. The disc was immediately stained in the field with 0.2 % di-methyl yellow in ethanol solution. The discs were labelled and placed in sealable plastic bags for transport to the laboratory.

4.2.2 Laboratory measurements

4.2.2.a Leaf area

The leaves of each harvested branch were removed, leaving the petiole on the branch. A sub-sample of 10 leaves was taken which represented the range of leaf size and age on the branch. These leaves were measured for projected area using a leaf area meter (Delta-T Devices Limited, Cambridge, UK). The remaining leaves were placed in a brown paper bag and dried at 35-40 °C for a minimum of 72 h before being placed in an 80 °C oven for 24 h. After area measurement, the sub-samples were also dried in this fashion.

Following drying, the bulk samples and sub-samples were allowed to cool overnight in a desiccator before being weighed separately. The weights of the sub-samples were used in conjunction with their area measurement to calculate specific leaf area (leaf area: leaf weight, $m^2\ kg^{-1}$) for each branch. This figure was then applied to the total weight (bulk sample plus sub-sample) for each branch to estimate branch leaf area.

4.2.2.b Sapwood area

The sapwood/heartwood boundary was marked on the discs taken from each tree (1.3 m and crown base). The outline of the disc (without bark) and the sapwood/heartwood boundary was traced onto tracing paper. This was then photocopied onto thick paper which was cut according to the wood disc outline. The leaf area meter was used to determine the cross-sectional area of stem from this outline (sapwood plus heartwood). The heartwood section was then cut out and its area determined. Sapwood area was calculated as the difference between stem area and heartwood area.

4.2.3 Sapwood hydraulic conductivity

Hydraulic conductivity of the sapwood was measured using the method outlined by Edwards and Jarvis (1982). Two stem sections approximately 0.6 m in length were removed from each sampled tree. One section was removed from below 1.3 m and the second section was taken from below green crown base. The sections were placed in humid plastic bags in the field before being transported to the laboratory where they were stored at 4 °C.

A section 0.3 m in length was cut from the middle of each sample. The stem sections were prepared by chiselling both the inlet and outlet sapwood surfaces. The stem section was placed between two 10 mm perspex plates and made watertight by tightening the six threaded rods and thumbscrews joining the two plates. A 10 mm soft black rubber tube was glued to the cambium to assist in sealing the stem section. Distilled water was deaerated using an ultrasonic horn (Branson Sonic Power, Danbury, Connecticut, USA). To remove embolisms which had formed in the sapwood during transport and preparation, the distilled water was applied to the stem section under a high constant head of pressure.

Outflow rate was measured until the flow rate had stabilised. It was assumed that this represented saturation of the sapwood. In addition, the absence or presence of air bubbles at the outlet end provided a visual aid for determining if sapwood saturation had been achieved. Depending on the size of the sample, this usually took 15-20 minutes. After the sapwood had been saturated, the outflow of water was collected and the volume recorded every two minutes. The length of the stem section was measured. Two water manometers connected to the inlet and outlet hoses measured the pressure differential across the stem section. Water viscosity values were obtained from tables using temperature measurements taken at the outlet end of the section. After the hydraulic conductivity measurements, 0.25% toluidine blue solution was passed through the stem section to determine the cross-sectional area of sapwood. Hydraulic conductivity (k) was calculated using Darcy's equation;

$$k = \frac{q\eta l}{A_s \Delta P} \qquad 4.1$$

where q is water flow ($m^3\ s^{-1}$), η is water viscosity (Pa s), l is length of stem section (m), A_s is cross-sectional area of sapwood (m^2) and ΔP is pressure potential (Pa). A linear change in flow rate with change in pressure gradient was taken as evidence that flow through the sapwood complied with the Darcy equation.

4.2.4 Analysis

A branch area - leaf area model for each crown zone was developed and used to estimate the leaf area across all tree diameter classes. Leaf area by crown zone and

by tree was estimated by summing the leaf area of individual branches.

Allometric relationships were modelled using the power function form (Causton 1985);

$$y = ax^b \qquad 4.2$$

Thus, a two-sided logarithmic transformation produces a linear relationship which can be analysed using linear regression analysis. A group regression procedure (McPherson 1990 p. 549) was used to determine the effect of site on the slope and intercept of the relationships. This procedure uses analysis of variance to test if the deviance of the model is significantly increased by generalising a and b across crown zones and sites for branch-level relationships and across sites for tree-level relationships. A visual analysis of plots of studentised residuals (residual divided by its standard error) against predicted values was used to check for systematic bias. The bias introduced by back-transforming logarithmic models was countered by calculating a bias correction factor for each model. The bias correction factor was calculated as the ratio of the actual sample mean to the mean of the back-transformed predicted values from the regression (Snowdon 1991).

Analysed stem variables were stem basal area (A_b), heartwood cross-sectional area (A_h), sapwood cross-sectional area (A_s), sum of branch basal area (A_{br}), and sapwood volume (V_s). Crown variables used were branch leaf area ($A_{l,br}$) and projected (one-sided) leaf area (A_l). Regression analyses were carried out using the GLM procedure in the SAS statistical package (SAS Institute Incorporated 1990).

Within the crown, the ratio of leaf area to sapwood area was expressed relative to the ratio measured at crown base by;

$$A_l : A_{s,rel} = \frac{A_l : A_{s,x}}{A_l : A_{s,cb}} \qquad 4.3$$

where A_l:$A_{s,x}$ is the ratio of leaf area to sapwood area at crown height x and A_l:$A_{s,cb}$ is the ratio of leaf area to sapwood area at crown base.

The height within the crown at which each leaf area – sapwood area ratio was measured was expressed in terms of relative crown height using;

$$H_{rel} = \frac{H_x - H_{cb}}{H_{tot} - H_{cb}} \qquad 4.4$$

where H_{rel} is the relative crown height, H_x is the height at which leaf area – sapwood area was measured, H_{cb} is the height of the crown base and H_{tot} is total tree height.

The influence of thinning on specific leaf area (SLA) ($cm^2\ g^{-1}$) was investigated using an unpaired *t*-test.

Regression analysis was used to explore the relationship between leaf area – sapwood area ratio and sapwood hydraulic conductivity. Values were log-transformed for linear regression analysis.

4.3 Results

4.3.1 Stem relationships and foliage characteristics

Sapwood area at breast height ($A_{s,1.3}$) ranged from 162.4 cm^2 to 340.3 cm^2 for the trees from the thinned stand and from 81.7 cm^2 to 307.4 cm^2 for the trees from the unthinned stand. Sapwood area (A_s; Figure 4.1a) and heartwood area (A_h; Figure 4.1b) were strongly related to stem cross-sectional area (A_b) at all points of sampling up the stem. Thinning treatment and crown zone did not influence this

relationship ($p > 0.05$).

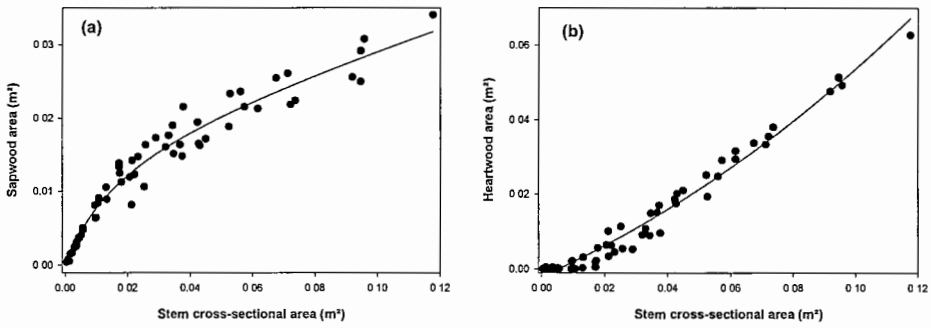


Figure 4.1 Relationship between stem cross-sectional area and (a) sapwood area and (b) heartwood area. Data from different tree heights and thinning treatments were pooled. The relationships were described by (a) a hyperbolic function ($r^2 = 0.96$), and (b) a quadratic function ($r^2 = 0.98$).

The mean rate of stem taper increased with increasing stem size (r^2=0.78; Figure 4.2) and this relationship was not influenced by thinning treatment.

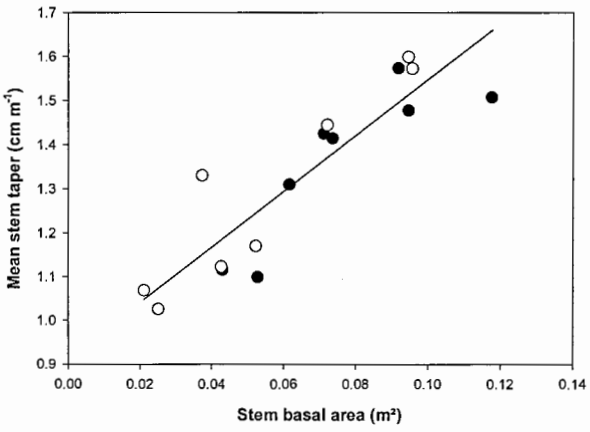


Figure 4.2 Rate of stem taper from breast height to tree tip as a function of tree size (stem cross-sectional area at breast height). Linear regression line shown was based on pooled data from the thinned (closed symbols) and unthinned (open symbols) stands, Goulds Country.

Sapwood area tapered from breast height to crown base for all trees (Figure 4.3). Tree size, expressed as sapwood area at breast height, did not affect the rate of taper. On average, a decrease of 19 % in sapwood area between breast height and crown base was observed.

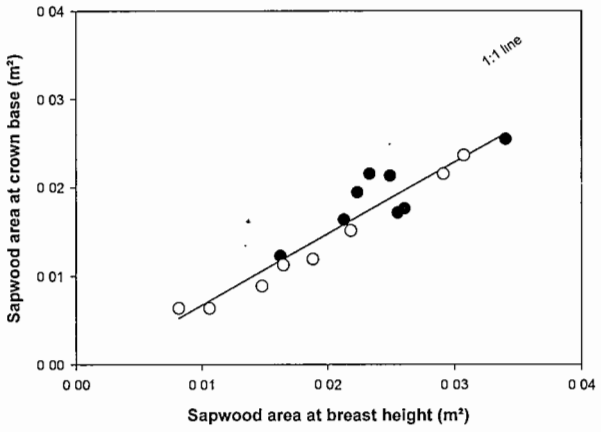


Figure 4.3 Sapwood taper from breast height to crown base. Data from thinned (closed symbols) and unthinned (open symbols) treatments were pooled for the linear regression; $y = 0.81x-0.0013$; $r^2 = 0.90$.

Branch sapwood area ($A_{s,br}$) was non-linearly related to stem A_s throughout the crown of trees from each thinning treatment (Figure 4.4).

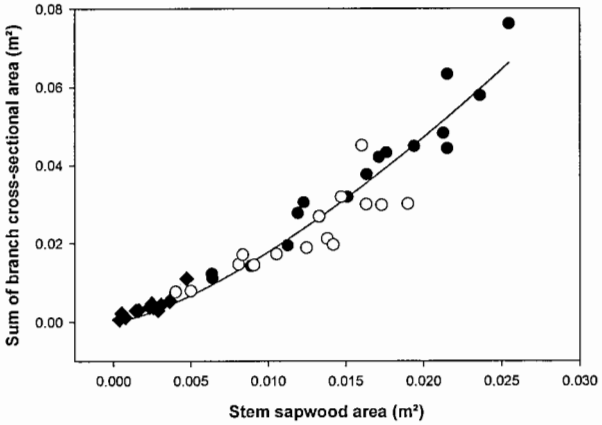


Figure 4.4 Relationship between stem sapwood area within the crown and the sum of branch cross-sectional area supported by the stem sapwood. Data pooled for thinned and unthinned treatments. Data shown for crown base (●), middle crown (○) and upper crown (♦). Displayed regression line; $y = 11.5x^{1.41}$; $r^2 = 0.94$.

No difference was found between the mean specific leaf area (SLA) of thinned and unthinned trees ($p > 0.05$). SLA decreased with crown height and varied significantly with canopy zone ($p < 0.01$; Table 4.2). The mean SLA of the lower zone was significantly higher than that of the middle and upper zones. While the mean SLA of the middle canopy zone was higher than that of the upper canopy zone, this difference was not significant.

Table 4.2 Mean specific leaf area ($m^2\ kg^{-1}$) for thinned and unthinned trees across all diameter classes by canopy zone, Goulds Country 1997. Mean standard errors are in parentheses.

Treatment	Lower canopy	Middle canopy	Upper canopy
thinned	4.58 (0.06)	4.10 (0.05)	3.94 (0.06)
unthinned	4.58 (0.07)	4.21 (0.06)	4.10 (0.06)

4.3.2 Leaf area - sapwood area relationships

The group regression procedure found a common slope across thinning treatment and canopy zones for the relationship between the natural logarithms of branch basal area (A_{br}) and branch leaf area ($A_{l,br}$). While the intercept of the relationship was common between branches from thinned and unthinned trees, it was necessary to use a different intercept for each canopy zone ($r^2 = 0.91$; Table 4.3).

Table 4.3 Values of parameters for a linear regression model of the natural logarithm of branch area and the natural logarithm of branch leaf area by crown zone, $\ln(A_{l,br})_i = (\bar{a} + a_i) + \bar{b}\ln(A_{br})$, for thinned and unthinned trees, Goulds Country.

Parameter	Effect	Details	Parameter value
Intercept	Mean ($\bar{a}$)		-7.06
	Zone (a_i)	*i*=lower	-0.61
		i=middle	0.20
		i=upper	0.00
Slope	Mean ($\bar{b}$)		1.18

Non-linear relationships between A_s and A_l were measured using both $A_{s,1.3}$ (Figure 4.5a) and $A_{s,cb}$ (Figure 4.5b). In both instances, thinning treatment did not influence the relationship. The relationship was stronger (and less curvilinear) at crown base compared with breast height. The mean ratio of leaf area to sapwood area (using $A_{s,1.3}$) in the thinned treatment was 0.51 m^2 cm^{-2}. In the unthinned treatment the mean ratio was 0.38 m^2 cm^{-2}. The difference between the two treatments was not significant (*t*-test; $p = 0.06$).

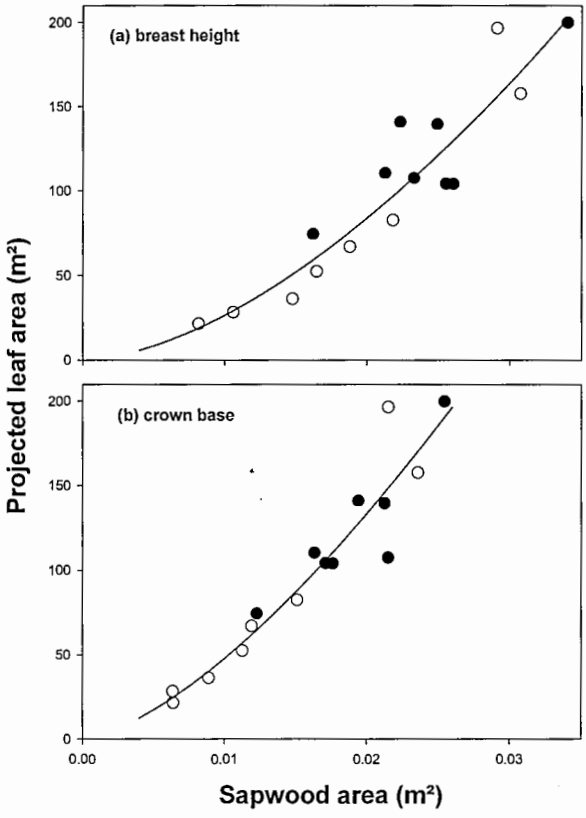


Figure 4.5 Relationship between sapwood area and projected leaf area for destructively sampled trees, Goulds Country 1997. Closed circles are thinned trees, open circles are unthinned trees. Figure (a) sapwood area at breast height, (b) sapwood area at crown base. Fitted regression lines to pooled (thinned and unthinned) data are; (a) $y = 55525x^{1.661}$, r^2=0.92, (b) $y = 43843x^{1.4819}$ r^2=0.95.

A non-linear relationship was found between A_s and A_l within the crown (Figure 4.6). This relationship was not affected by thinning treatment. Sapwood area in the lower crown supported a greater amount of leaf area per unit sapwood area compared with the upper crown.

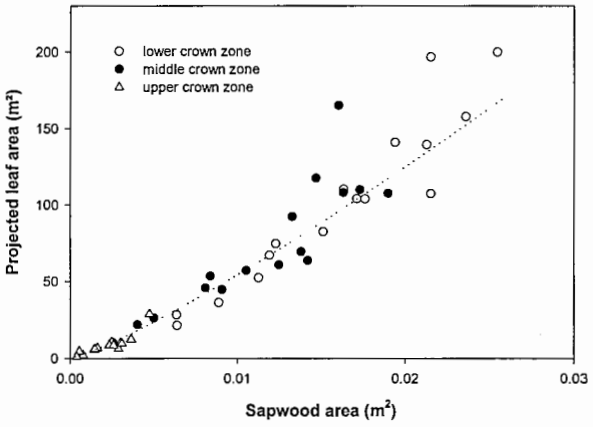


Figure 4.6 Leaf area - sapwood area relationship within the crown. Data pooled for thinned and unthinned trees, Goulds Country trial 1997. Pooled regression relationship; $y = 13748x^{1.20}$, $r^2 = 0.96$.

The ratio of leaf area to sapwood area relative to the ratio at crown base decreased from crown base with crown height in trees from the thinned stand (Figure 4.7). In the unthinned stand, this ratio increased from crown base to one-third of crown height (Figure 4.7). Trees from the unthinned stand had a significantly higher ratio at one-third of crown height than trees from the thinned stand (t-test, $p < 0.05$). The relative ratio at two-thirds of crown height was greater in trees from the unthinned stand compared with that of the thinned stand but this was not significant (t-test, $p = 0.108$).

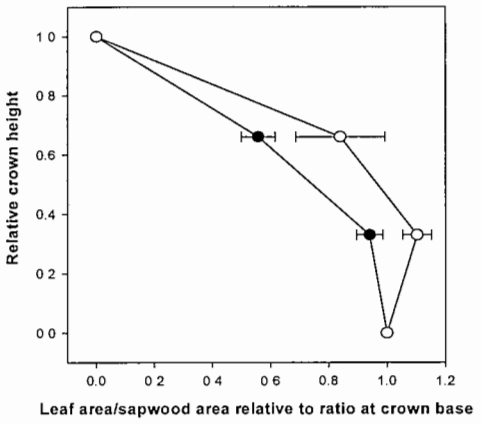


Figure 4.7 Change in the ratio of leaf area to sapwood area throughout the crown, relative to the ratio at crown base for thinned (closed symbols) and unthinned (open symbols) stands. Error bars show mean standard errors.

4.3.3 Sapwood hydraulic conductivity

Sapwood hydraulic conductivity (k) values were unable to be obtained for all of the sixteen sampled trees due to technical problems. The k at crown base was successfully measured for thirteen trees. Five of these trees were also measured for k at breast height. While unable to be tested statistically, all five trees showed higher k at crown base compared with breast height (Table 4.4). On average, the increase in k from breast height to crown base was close to 100 %. A weak (r^2=0.30) yet significant ($p < 0.05$) relationship between leaf area – sapwood area ratio and k at crown base was not influenced by thinning treatment (Figure 4.8).

Table 4.4 Sapwood hydraulic conductivity at breast height and crown base, Goulds Country thinning trial.

Tree ID	Sapwood hydraulic conductivity ($m^2 \times 10^{12}$)	
	Breast height	Crown base
control-1	2.64	5.77
control-8	4.54	8.95
thin-1	7.27	13.64
thin-2	4.62	7.13
thin-3	6.46	14.83

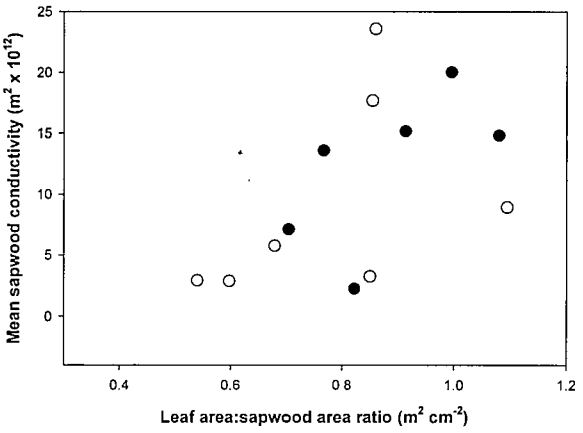


Figure 4.8 Relationship between leaf area - sapwood area ratio and sapwood hydraulic conductivity at crown base for trees from thinned (closed symbols) and unthinned (open symbols) stands, Goulds Country. Sapwood areas used in the hydraulic conductivity measurement were used in calculating leaf area – sapwood area ratios.

4.4 Discussion

4.4.1 Leaf area – sapwood area ratio

In this study, trees from the thinned treatment had higher leaf area – sapwood area (A_l:A_s) ratios than trees from the unthinned treatment. However, the relationship between leaf area and sapwood area was found to be non-linear. Consequently, the A_l:A_s ratio was dependent on tree size, rather than silvicultural treatment *per*

se. Subsequent analysis of the relationship between leaf area and sapwood area in *E. nitens* across a wide range of sites under different silvicultural regimes has shown a consistent, non-linear relationship not influenced by site or treatment (Medhurst et al. 1999, see Chapter 5). The results of the present study support the conclusions based on Dean and Long (1986) and Long and Smith (1989) that reported differences in A_l - A_s ratios with site quality (Keane and Weetman 1987), climate (Mencuccini and Grace 1995), stand density (Brix and Mitchell 1983) and growth rate (Espinosa-Bancalari et al. 1987) may be explained when A_l is estimated as a non-linear function of A_s. However, the non-linearity of the relationship between A_s and A_l with *Pinus contorta* var. *latifolia* (Engel.) Critch was in relation to A_s at breast height and attributed to sapwood area taper in the stem and varying lengths of crown-free stem (Dean and Long 1986). In the present study, non-linearity was also found using A_s at crown base despite sapwood area taper from breast height to crown base (Figure 4.3).

The leaf area - sapwood area relationship was stronger (and more linear) at crown base compared with breast height. $A_{s,cb}$ has been found to more closely reflect the water requirements of the crown and hence be the preferred point for leaf area estimation (Espinosa-Bancalari et al. 1987; Robichaud and Methven 1992). However, $A_{s,1.3}$ was able to explain 92% of the variation in A_l and would be adequate as a scalar for A_l estimation in *E. nitens*. Similar findings have been reported for young *E. nitens* and *E. globulus* (White et al. 1998).

Differences in the A_l:A_s ratio at the two points of measurement were due to tapering of sapwood area between breast height and crown base. Other studies have also reported sapwood taper along this section of stem (Waring et al. 1982; Dean and Long 1986). However, the 19% reduction in sapwood area found in this

study was less than those reported for *Pinus ponderosa* Dougl. (42%, Waring et al. 1982) and *P. taeda* (48%, Blanche and Hodges 1985). The degree of reduction in sapwood area in *E. nitens* was independent of tree size and thinning treatment. An increase in allocation of sapwood to water storage (Zimmerman 1983) with increasing distance below the crown base would contribute to the change in A_l:A_s. In other non-linear relationships between A_l and A_s (Dean and Long 1986; Long and Smith 1988; Long and Smith 1989; Pereira et al. 1997), inclusion of a variable describing height to crown base or height to mid-point of the crown was significant in the A_l - A_s models. In *E. nitens* however, including crown length in A_l - A_s models did not significantly improve the goodness-of-fit (see Chapter 5).

Within the crown of trees from the thinned stand, the amount of leaf area supported per unit sapwood area decreased with height. Differences in the change in leaf area with sapwood area throughout the crown exist between species. A constant ratio between leaf area and sapwood area throughout the crown has been shown for a range of western coniferous species (Kaufmann and Troendle 1981; Waring et al. 1982). In contrast, a decreasing ratio with crown height was found in *Pseudotsuga menziesii* (Mirb.) Franco (Brix and Mitchell 1983). In the present study, a lower A_l:A_s ratio in the upper crown may be due to greater irradiance and consequently higher transpiration rates per unit leaf area in this region of the crown. It might then be expected that the improved light environment following thinning would alter the pattern of A_l:A_s ratio throughout the crown. No differences in sapwood area taper were found between treatments, therefore differences in A_l:A_s within the crowns of trees in thinned and unthinned stands were presumably due to differences in the vertical distribution of foliage. This is explored further in Chapter 6.

4.4.2 Specific leaf area

The differences in SLA with tree age and crown zone in this study highlight the importance of stratification in any estimation of tree leaf area from leaf weight (Keane and Weetman 1987). Mean SLA was greatest (*ie.* thinner leaves) in the lower crown zone and least (*ie.* thicker leaves) in the upper crown zone. This pattern may be linked to available light levels (Bartelink 1997; Gratani 1997) where a higher mean SLA in lower reaches of the crown is a morphological response to reduced light availability with less carbon invested per unit light intercepted (Beadle 1993).

4.4.3 Hydraulic conductivity of sapwood

Thinning treatment did not alter the relationship between leaf area and sapwood area at either breast height or crown base. However, the non-linear nature of the relationship indicated that larger, fast-growing trees were able carry a greater amount of leaf area per unit area of sapwood and hence show a higher A_l:A_s ratio, independently of thinning treatment. Sapwood conductivity at crown base was positively correlated with A_l:A_s ratio, and hence with growth rate. This result provides support for the hypothesis that the relationship between leaf area and sapwood area is dependent on the transpiration rate of the foliage and the hydraulic conductivity of the sapwood (Whitehead et al. 1984a). Equating the tree transpiration rate to volume flow based on Darcy's law raises the expectation that the ratio of leaf area to sapwood area is positively related to sapwood hydraulic conductivity (Whitehead et al. 1984a). Consistent with this, a positive relationship between the two variables was shown for *E. nitens* in this study.

Sapwood hydraulic conductivity increased by approximately 100 per cent from

breast height to crown base, while sapwood area decreased by 19 per cent. This suggests that the efficiency of water transport through the sapwood increased by 60 per cent along this length. This is supported by the regression equations given in Figure 4.5 which show that the sapwood area at crown base will support, on average, close to 60 per cent more leaf area than a similar amount of sapwood area at breast height. These results suggest that sapwood hydraulic conductivity can explain the variation in the relationship between leaf area and sapwood area in *E. nitens*. A strong association between the ratio of leaf area and sapwood area and sapwood hydraulic conductivity was shown for *Picea sitchensis* (Bong.) Carr and *P. contorta* (Whitehead et al. 1984a).

The proportion of sapwood actively involved in water transport increases with tree height (Shelburne and Hedden 1996) as greater amounts of sapwood are used for water storage in the lower sections of the stem (Zimmerman 1983). A decrease in the number of growth rings in the sapwood with increasing stem height (Brix and Mitchell 1983; Pothier et al. 1989) is also likely to improve hydraulic conductivity due to a lower proportion of denser latewood. The relationships between stem cross-sectional area, sapwood area and heartwood area did not change as a result of thinning. A possible decrease in the number of growth rings in the sapwood may have occurred after thinning due to faster diameter growth rates (Chapter 3). However, this was not specifically investigated as part of this study.

4.5 Conclusions

This study tested the hypothesis that the relationship between leaf area and sapwood area in *E. nitens* is affected by thinning treatment and could possibly

explain the observed differences in growth rate. However, no difference in the relationship between leaf area and sapwood area was found eight years after thinning. This result suggests that a single regression equation can be used to predict leaf area of trees in thinned and unthinned stands. This is explored more fully in Chapter 5. The finding that the relationship across the sapwood area range measured was non-linear implies a causal relationship between growth rate and A_l:A_s. Positive correlations between A_l:A_s and site quality (Whitehead 1978; Brix and Mitchell 1983; Binkley 1984) have led to speculation that increasing limited resources will increase sapwood hydraulic conductivity which will feed-forward to an increase in A_l:A_s (White et al. 1998). That large trees in this study had greater hydraulic conductivity and higher A_l:A_s lends support to this argument that resource capture, and hence growth rate, influence sapwood hydraulic conductivity.

Chapter 5. Allometric relationships for *E. nitens* plantations

5.1 Introduction

Allometry is an empirically-based description of the proportional change of one character in relation to another. In strict terms it refers to relationships based on the equation (after Causton 1985):

$$y = ax_1^{b1}x_2^{b2}...x_n^{bn} \qquad 5.1$$

In a double logarithm plot, the relationship is linear:

$$\log y = \log a + b_1 \log x_1 + b_2 \log x_2 ... b_n \log x_n \qquad 5.2$$

Allometry has been used to describe relationships between biomass components of trees of a uniform age within individual sites (eg. Whitehead 1978; Fownes and Harrington 1992; Pereira et al. 1997; Reed and Tomé 1998). Relationships between tree structural components such as the ratio of foliage mass to sapwood cross-sectional area (Albrektson 1984), foliage mass to stem mass (Cromer and Jarvis 1990), below-ground to above-ground biomass (Reed et al. 1995; Misra et al. 1998a) and branch length to branch diameter (Ford 1985) have also been described.

Functional significance has been attached to such relationships. Engineering principles and the requirement of plant parts for physical support have been used to explain the observed ratios between above- and below-ground biomass components of trees and observed relationships between tree crown-size and the height to diameter ratio of tree stems (West et al. 1989; Niklas 1992). The

observed relationships between leaf area and the cross-sectional area of stem and branch sapwood area have been explained in terms of transport requirements for water and volumetric flow rates predicted by Darcy's law (Shinozaki et al. 1964a; b; Whitehead et al. 1984a).

Allometric relationships can be tools of great convenience. For example direct measurement of leaf area is both destructive and impractical for use in forest canopies. However, leaf area is a fundamental variable of canopy structure and must be known for predictions of canopy photosynthesis, transpiration and light interception. Allometry is commonly applied to estimate leaf area in forest studies (Pereira et al. 1997). Allometry also has been used in process-based tree growth models as a means of allocating biomass based on relationships between woody biomass components and leaf area. (eg. Mäkelä 1986; Landsberg and Waring 1997; Bartelink 1998b). Alternative models for allocating biomass require greater phenomenological detail about the coordination of biomass partitioning and substrate transport (eg. ECOPHYS, Rauscher et al. 1990) that makes model implementation more difficult.

The utility of allometric relationships depends on how applicable they are to trees of different ages or from different sites, and the extent to which this variation can be predicted using site attributes. Allometric relationships between tree components have been shown to vary with species (Kaufmann and Troendle 1981), age (Albrektson 1984) and site conditions (Espinosa-Bancalari et al. 1987; Shelburne et al. 1993; Berninger and Nikinmaa 1997). Nevertheless, in some cases, consistent relationships have been found for some species across a range of sites (eg. Pastor et al. 1984; Bartelink 1996; 1997) and for trees of different ages within a single site (eg. Pereira et al. 1997).

E. nitens plantations are managed for a range of wood products. Silvicultural techniques used in these plantations can include fertilisation (Turnbull et al. 1997), irrigation (Honeysett et al. 1996) and thinning (Gerrand et al. 1997b). The plantations also experience weed infestation to varying extents (Hunt et al. 1999). While each of these factors can affect plantation growth, their impact on tree allometry is unknown. This chapter describes an analysis of structural relationships using data from 19 different *E. nitens* plantations and tests how these relationships change with growing conditions and silvicultural treatment.

5.2 Materials and methods

5.2.1 Study sites

Data were collected from 13 post-canopy closure and 6 pre-canopy closure *E. nitens* plantations in Tasmania. The sites represented a range of site quality, stand age and stand density (Table 5.1). The Goulds plantation (GO), sampled at age 6 years, was planted on an ex-pasture site of high fertility. Sampling at the Lewisham plantation was from both irrigated (LW-I) and rain-fed (LW-R) sites and was carried out at ages 2, 3 and 6 years. The major limitation to growth at this site was available soil water (Honeysett et al. 1996). Irrigation was scheduled using measurements of soil water deficit and delivered with microsprinklers at a rate of 5 mm h^{-1}. Supplementary irrigation was necessary on occasion in LW-R to prevent death due to severe drought stress (Honeysett et al. 1996). Wyena-A (WY-A) plantation was planted at a rate of 1000 stems ha^{-1}, had low soil nutrient status and had not achieved full canopy closure at time of sampling at age 7 years (Cherry et al. 1998). Sampling was carried out in four separate sites at the Creekton plantation, each of which had different site preparation and fertilizer

treatment in the first three years post-planting (Turnbull et al. 1997).

Table 5.1. Stand descriptions of the *E. nitens* sites used for leaf area and sapwood area sampling. The sites are listed on the basis of age at last measurement.

Site and code	Grid reference	Age (years)	Planted stocking (stems ha^{-1})	Annual rainfall (mm)	Altitude (m asl)	Soil nutrient status	Fertiliser treatment N:P:K (kg ha^{-1})
Wyena – weeds (WY-B)	41° 12' S 147° 16' E	4	1000	1020	250	moderate	200:400:0
Wyena – no weeds (WY-C)	41° 12' S 147° 16' E	4	1000	1020	250	moderate	200:400:0
Goulds (GO)	43° 18' S 147° 01' E	6	1430	950	100	high	200:120:0
Lewisham - rain-fed (LW-R)	42° 49' S 147° 36' E	2/3/6	1430	900[1]	20	moderate	400:120:0
Lewisham – irrigated (LW-I)	42° 49' S 147° 36' E	2/3/6	1430	1400	20	moderate	400:120:0
Wyena A (WY-A)	41° 10' S 147° 17' E	7	1000	1020	150	low	200:120:0
Creekton B (CK-B)	43° 21' S 146° 54' E	7	1430	1375	110	moderate	300:120:0
Creekton C (CK-C)	43° 21' S 146° 54' E	7	1430	1375	110	moderate	100:120:0
Creekton N (CK-N)	43° 21' S 146° 54' E	7	1430	1375	110	moderate	0:0:0
Creekton F (CK-F)	43° 21' S 146° 54' E	8	1430	1375	110	moderate	0:120:0
Wyena D (WY-D)	41° 12' S 147° 16' E	7/8	1000	1020	130	high	200:400:0
Lisle (LI)	41° 13' S 147° 22' E	9	1389	1055	220	high	0:0:0
Goulds Country (GC-200)	41° 05' S 148° 06' E	13	1143	1070	120	moderate	180:80:0
Goulds Country (GC-725)	41° 05' S 148° 06' E	13	1143	1070	120	moderate	180:80:0

[1]includes some supplementary irrigation

All four sites at Creekton were unthinned at the time of sampling. CK-B, CK-C and CK-N were sampled at age 7 years. CK-F was sampled at age 8 years. The Lisle site (LI) was sampled at age 9 years, immediately prior to the first thinning operation. The site was planted at 1389 stems ha^{-1} and no fertilizer was applied. Sampling in the 13-year-old Goulds Country plantation was from both thinned (GC-200) and unthinned (GC-725) sites. Sampling took place 7 years after thinning. The plantation was planted at 1143 stems ha^{-1} and was thinned to 200 stems ha^{-1}. The unthinned site had 725 stems ha^{-1} when sampled. Wyena-B (WY-B) was a plantation with heavy *Acacia dealbata* Link. weed infestation. Sampling was at age 4 years. Wyena-C (WY-C) was a nearby site free of *A. dealbata*. Sampling was also at age 4 years. Wyena-D (WY-D) was a site with a high level of *A. dealbata* infestation and was sampled at ages 7 and 8 years.

5.2.2 Destructive sampling

The destructive sampling was carried out as part of four separate studies (see Cherry et al. 1998; White et al. 1998; Hunt 1999). However, a similar protocol was followed in each study. Five to eight trees were sampled from each site.

To ensure sampling across the range of tree sizes, the diameter distribution at each site was divided into classes and a tree selected at random from each of the classes. The diameter distribution of sites studied by Cherry et al. (1998) was determined by a plot of 84 trees (7 rows by 12 trees) established at the centre of each site. White et al. (1998) used three 30-tree plots (5 rows by 6 trees) to determine diameter distribution. Hunt (1999) used three diameter classes to randomly select trees from the WY-D plantation at age seven years and five

diameter classes for selecting trees in WY-D (age eight years), WY-B, and WY-C. The diameter distribution was established from 22 plots each approximately 192 m^2 (Hunt et al. 1999). Diameter distribution of the GC-200 stand was based on four 0.1 ha plots (80 trees). Sampling in the GC-725 stand was restricted to the best 200 stems ha^{-1} (as identified at time of thinning) and the diameter distribution of these trees was determined from four 0.1 ha plots (80 trees). The diameter distribution of the LI and CK-F sites was each obtained using twelve 0.08 ha plots. At LI there was an average of 84 trees $plot^{-1}$ and at CK-F there was an average of 100 trees $plot^{-1}$. A description of the sampled trees from each site is outlined in Table 5.2.

The method used for destructive sampling at all sites is described in Chapter 4. In addition, the angle from the vertical (to the nearest 5 degrees) and azimuth sector (north-east, east-south, south-west and west-north) was recorded for each live branch on trees sampled from the CK-F, LI, GC-200 and GC-725 sites.

The methods used for laboratory measurements of sapwood area and leaf area are described in Chapter 4.

Table 5.2. Sample tree descriptions for the 6 pre-canopy closure and 13 post-canopy closure sites.

Site	No.	DBH (cm)	Height (m)	Sapwood area per tree (m^2x10^4)*	Leaf area per tree (m^2)**	Source
			Pre-canopy closure trees			
LW-R @ 2 yrs	6	0.6 - 4.2	1.4 - 4.0	0.3 - 13.9	2.2 - 19.7	b
LW-R @ 3 yrs	6	3.3 - 10.9	4.0 - 6.8	8.6 - 93.3	6.2 - 57.1	b
LW-I @ 2 yrs	6	1.1 - 5.4	1.9 - 4.0	1.0 - 22.9	1.9 - 21.3	b
LW-I @ 3 yrs	6	5.7 - 11.0	5.4 - 7.2	25.5 - 95.0	11.1 - 39.5	b
WY-B	5	6.2 - 13.0	7.3 - 11.0	25.3 - 96.2	7.2 - 38.7	c
WY-C	5	4.3 - 11.1	6.9 - 11.2	9.0 - 67.0	7.6 - 30.5	c
			Post-canopy closure trees			
GO	6	9.9 - 21.2	13.2 - 18.9	37.8 - 171.4	10.5 - 102.2	a
LW-R @ 6 yrs	6	7.7 - 16.6	6.9 - 12.4	26.7 - 105.1	7.1 - 70.5	b
LW-I @ 6 yrs	6	9.0 - 20.2	10.7 - 14.9	51.2 - 145.7	15.2 - 103.9	b
WY-A	6	4.3 - 10.3	4.2 - 7.9	11.0 - 43.4	0.8 - 3.3	a
CK-B	6	6.5 - 17.7	9.2 - 15.1	23.4 - 137.8	5.9 - 67.8	a
CK-C	6	7.7 - 22.9	11.2 - 19.0	27.0 - 147.2	7.6 - 80.6	a
CK-N	6	3.6 - 15.4	4.6 - 12.4	7.0 - 114.7	0.6 - 55.7	a
CK-F	6	7.4 - 26.5	11.5 - 21.1	22.7 - 194.0	6.0 - 108.4	d
WY-D @ 7 yrs	6	15.3 - 24.6		107.6 - 219.8	25.8 - 90.6	c
WY-D @ 8 yrs	5	12.0 - 25.2	15.9 - 24.4	35.3 - 234.5	4.9 - 73.7	c
LI	6	6.8 - 32.8	10.8 - 26.1	26.7 - 329.4	1.6 - 127.0	d
GC-200	8	23.4 - 38.7	20.6 - 24.6	162.4 - 340.3	74.4 - 199.9	d
GC-725	8	16.4 - 34.9	15.6 - 21.6	81.7 - 307.4	21.5 - 196.5	d

* sapwood area measured at 1.3 m stem height
** projected or one-sided
a Cherry et al. (1998)
b White et al. (1998)
c Hunt (1999)
d Medhurst (unpublished data)

5.2.3 Analysis

Sites were categorised either as pre- or post-canopy closure sites. Canopy closure was defined as the stage when the crowns of most adjacent trees touch. For this

analysis, sites aged 4 years or less were classed as pre-canopy closure stands.

At each site a branch area - leaf area model for each crown zone was developed and used to estimate the leaf area across all tree diameter classes. Leaf area by crown zone and by tree was estimated by summing the leaf area of individual branches.

Crown projection area was calculated for trees from the CK-F, LI, GC-200 and GC-725 sites. The maximum branch projection length from each of the four azimuth sectors was used to calculate crown projection area for each sector. Sector areas were then summed to give an estimate of total crown projection area.

Leaf area density (ρ_L) was estimated using the formula:

$$\rho_L = \frac{A_{l,z}}{V_z} \qquad 5.3$$

where $A_{l,z}$ is leaf area in crown zone z, and V_z is volume of crown zone z. Crown zone volume was estimated by assuming that the lower crown zone could be described as a cylinder and that the middle and upper crown zones combined were shaped like a cone with a basal area equal to crown projection area and a height equal to twice the zone length. A visual comparison of this model with actual crown shape was done using a two-dimensional map of branching for GC trees (Medhurst, unpublished data). The model was shown to overestimate volume of the lower crown zone and underestimate volume of the middle and upper crown zones. Crown zone volumes were adjusted using the ratio of the model's cross-sectional area to the approximate cross-sectional area of the branch map as a correction factor.

Allometric relationships were modelled using the power function form (Causton

1985);

$$y = ax^b \qquad 5.4$$

The method described in Chapter 4 was used to analyse each relationship.

Branch variables analysed were branch diameter (D_{br}), branch cross-sectional area at 40 mm from stem (A_{br}), and branch length (L_{br}). Stem variables (Table 5.3) analysed were diameter over-bark at breast height ($D_{1.3}$) and crown base (D_{cb}), basal area at breast height ($A_{b,1.3}$) and crown base ($A_{b,cb}$), heartwood area ($A_{h,1.3}$ and $A_{h,cb}$), sapwood area ($A_{s,1.3}$ and $A_{s,cb}$), sum of branch sapwood area ($A_{s,br}$), and total height (H_t). Crown variables used were crown length (L_c) and projected (one-sided) leaf area (A_l). Regression analyses were carried out using the GLM procedure in the SAS statistical package (SAS Institute Incorporated 1990).

Table 5.3 Summary statistics for tree variables (n = 115).

Variable	Mean	Mean SE	Min.	Max.
$D_{1.3}$ (cm)	14.1	0.8	0.6	38.7
D_{cb} (cm)	11.1	0.6	2.3	29.3
H_t (m)	12.2	0.6	1.4	26.1
L_c (m)	8.1	0.4	1.4	16.1
$A_{b,1.3}$ (cm^2)	214.5	23.0	0.3	1176.3
$A_{b,cb}$ (cm^2)	127.2	13.4	4.2	674.3
$A_{s,1.3}$ (cm^2)	93.0	7.4	0.3	340.3
$A_{s,cb}$ (cm^2)	76.2	5.9	3.0	279.6
$A_{h,1.3}$ (cm^2)	121.6	16.1	0.0	836.0
$A_{s,br}$ (cm^2)	3.4	0.2	0.1	44.2
A_l (m^2)	41.2	3.8	0.6	199.9

5.3 Results

5.3.1 Stem relationships

The amount of sapwood area at crown base ($A_{s,cb}$) was proportional to the amount at breast height ($A_{s,1.3}$) for post-canopy closure trees (Figure 5.1). Group regression analysis showed that site was not a significant variable in this relationship. The intercept of the general regression equation was not statistically significant ($p > 0.05$), so sapwood taper was described with the following equation;

$$A_{s,cb} = 0.77\, A_{s,1.3} \qquad (n=75,\ r^2 = 0.94) \qquad 5.5$$

No measurements of sapwood area were taken between these two reference points on the stem so the rate of sapwood taper with stem height is unknown.

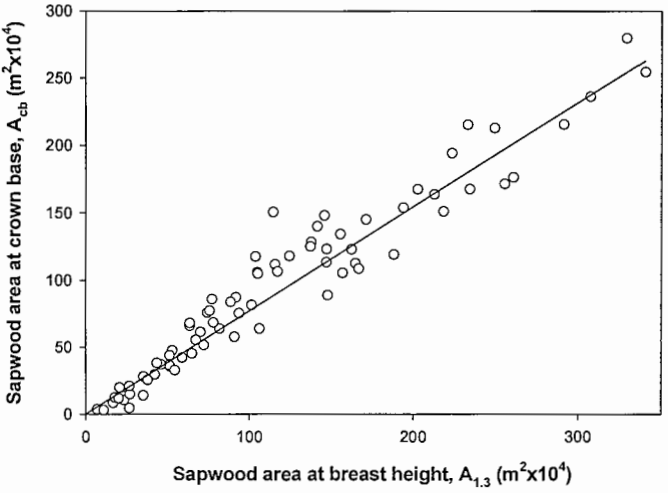


Figure 5.1 Sapwood taper from breast height to crown base. Data pooled from twelve post-canopy closure sites (n=75) (no crown base data for WY-D age 7 yrs). See equation 5.5 for regression model.

Branch sapwood area ($A_{s,br}$) was non-linearly related to $A_{s,cb}$ for post-canopy closure trees. The log-log relationship was independent of site. Back-transformation of the model gave the following with a bias correction factor of 1.06;

$$A_{s,br} = 1.13 A_{s,cb}^{1.09} \qquad (n=75, r^2=0.95) \qquad 5.6$$

$A_{s,cb}$ was strongly related to basal area at crown base ($A_{b,cb}$) and $A_{s,1.3}$ was strongly related to basal area at breast height ($A_{b,1.3}$) (Figure 5.2a). The slope and intercept of the two log-log relationships were common across all post-canopy closure sites (n=75, r^2=0.97 and n=81, r^2=0.95 respectively). Both the breast height and crown base data were adequately explained using one model. Back-transformation of the pooled regression gave the following relationship with a calculated bias correction factor of 0.98;

$$A_s = 1.34 A_b^{0.82} \qquad (n=156, r^2=0.95) \qquad 5.7$$

The log-log relationship between basal area and heartwood area was stronger at breast height than at crown base for post-canopy closure trees (Figure 5.2b).

In both cases the relationship was independent of site. Breast height and crown base data could not be explained using one model because of significantly different intercepts. The bias correction factors for back-transformation of the breast height and crown base models were 1.05 and 1.41 respectively. The individual models for breast height and crown base were;

$$A_{h,1.3} = 0.06 A_{b,1.3}^{1.32} \qquad (n=73, r^2=0.92) \qquad 5.8$$

$$A_{h,cb} = 0.02 A_{b,cb}^{1.42} \qquad (n=53, r^2=0.74) \qquad 5.9$$

Diameter at breast height ($D_{1.3}$) was related to tree height (H_t) (Figure 5.3a).

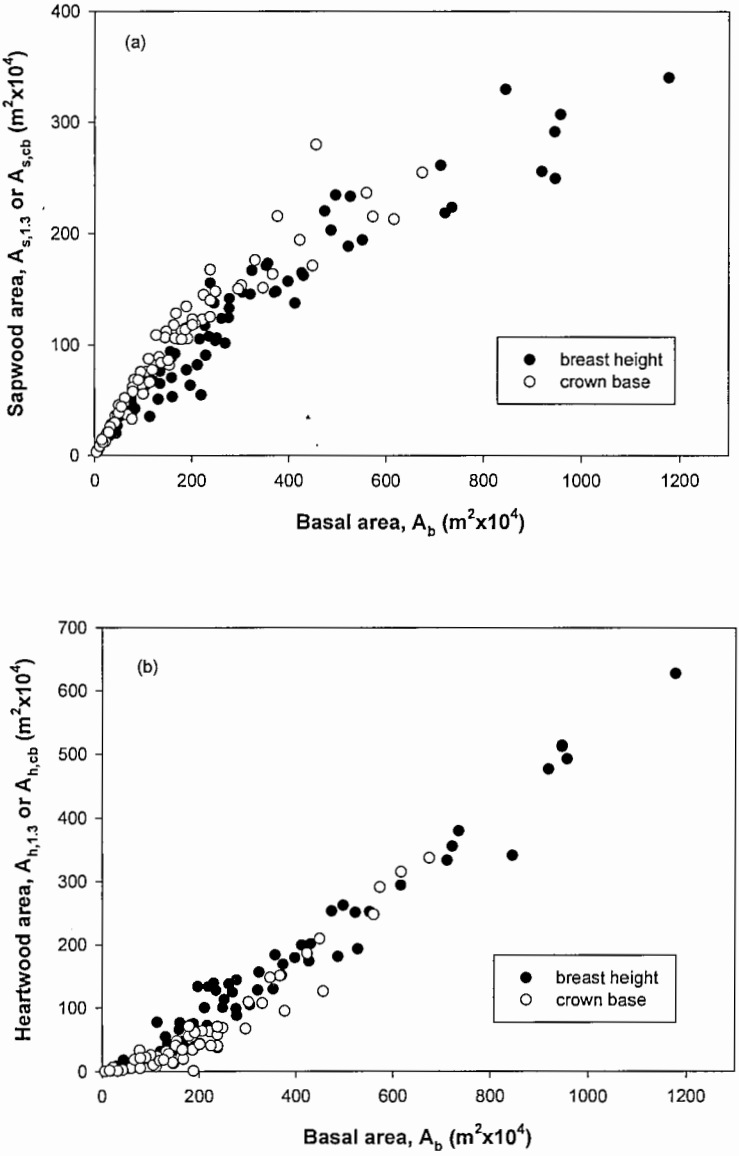


Figure 5.2 The relationship between stem basal area and (a) sapwood or (b) heartwood area for post-canopy closure sites. Separate plots are shown for breast height (n=81) and crown base (n=75). For sapwood area, the relationship was adequately explained by one model.

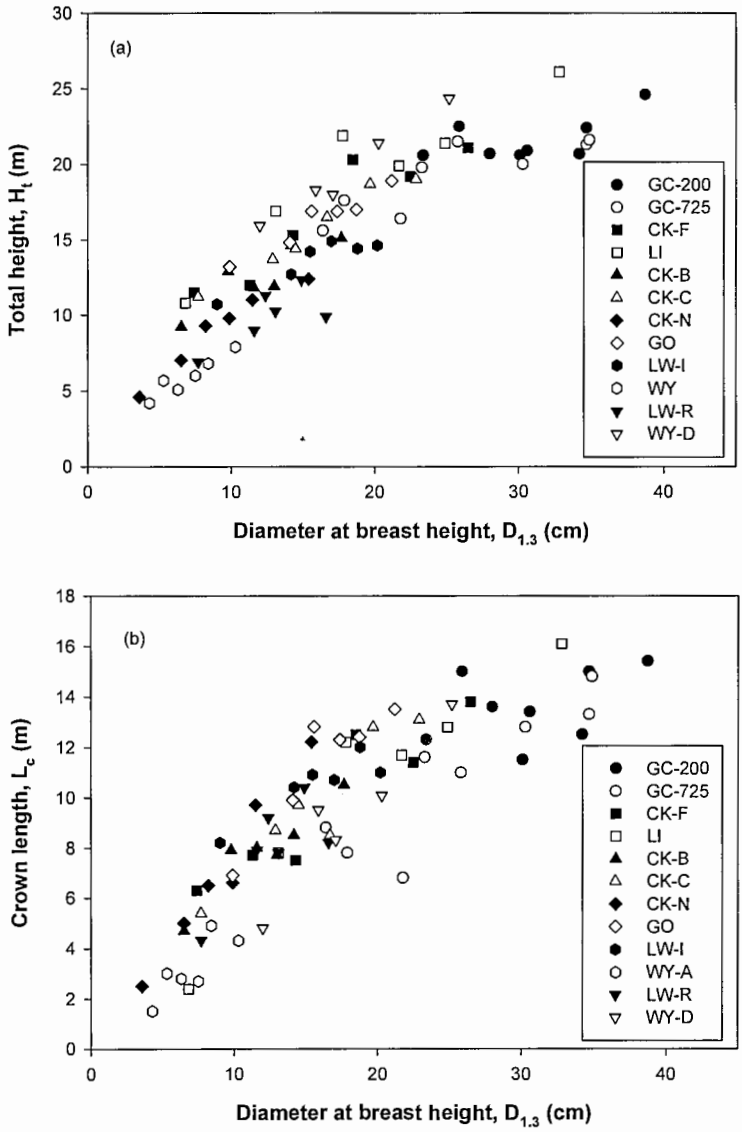


Figure 5.3 The relationship between diameter at breast height and (a) tree height (n=75) or (b) crown length (n=75) for post-canopy closure sites. Separate plots are shown for each site (no WY-D age 7).

The log-log linear regression (n=75, r^2=0.97) had a common slope, but significantly different intercepts across post-canopy closure sites (Table 5.4). A non-linear asymptotic model (West 1979) provided a good fit of the untransformed data pooled from both pre- and post-canopy closure sites.

$$H_t = \frac{D_{1.3}}{0.77 + (0.019 * D_{1.3})} \qquad (n=109,\ r^2=0.98) \qquad 5.10$$

5.3.2 Leaf area - sapwood area relationships

There was a change in the A_l - $A_{s,1.3}$ relationship in young trees (pre-canopy closure) with age (Figure 5.4). The amount of leaf area carried per unit sapwood area decreased with age until at age 4 years when the trees were close to the modelled relationship of the post-canopy closure sites (see below).

Table 5.4 Linear regression equations for post-canopy closure sites using natural logarithms of parameters.

Site	Equation	Site	Equation
Stem diameter v. tree height		*Stem diameter v. crown length continued*	
GO	ln(H) = 1.291 + 0.541*ln(D)	CK-F	ln(L) = -0.253 + 0.915*ln(D)
LW-R6	ln(H) = 0.920 + 0.541*ln(D)	WY-D8	ln(L) = -0.447 + 0.915*ln(D)
LW-I6	ln(H) = 1.125 + 0.541*ln(D)	LI	ln(L) = -0.412 + 0.915*ln(D)
WY-A	ln(H) = 0.731 + 0.541*ln(D)	GC-200	ln(L) = -0.517 + 0.915*ln(D)
CK-B	ln(H) = 1.194 + 0.541*ln(D)	GC-725	ln(L) = -0.582 + 0.915*ln(D)
CK-C	ln(H) = 1.267 + 0.541*ln(D)	*Branch diameter v. branch length*	
CK-N	ln(H) = 1.003 + 0.541*ln(D)	GO	ln(L) = -1.826 + 0.933*ln(D)
CK-F	ln(H) = 1.299 + 0.541*ln(D)	LW-I6	ln(L) = -1.687 + 0.824*ln(D)
WY-D8	ln(H) = 1.414 + 0.541*ln(D)	WY-A	ln(L) = -2.243 + 0.985*ln(D)
LI	ln(H) = 1.388 + 0.541*ln(D)	CK-B	ln(L) = -1.952 + 0.969*ln(D)
GC-200	ln(H) = 1.225 + 0.541*ln(D)	CK-C	ln(L) = -1.823 + 0.907*ln(D)
GC-725	ln(H) = 1.212 + 0.541*ln(D)	CK-N	ln(L) = -2.039 + 0.968*ln(D)
Tree height v. crown length		CK-F	ln(L) = -1.960 + 0.935*ln(D)
GO	ln(L) = -2.111 + 1.621*ln(H)	WY-D8	ln(L) = -1.936 + 0.971*ln(D)
LW-R6	ln(L) = -1.660 + 1.621*ln(H)	LI	ln(L) = -2.265 + 1.023*ln(D)
LW-I6	ln(L) = -1.869 + 1.621*ln(H)	GC-200	ln(L) = -1.660 + 0.811*ln(D)
WY-A	ln(L) = -1.756 + 1.621*ln(H)	GC-725	ln(L) = -1.639 + 0.801*ln(D)
CK-B	ln(L) = -2.047 + 1.621*ln(H)	*Stem diameter v. crown volume*	
CK-C	ln(L) = -2.194 + 1.621*ln(H)	CK-F	ln(V) = -1.423 + 1.643*ln(D)
CK-N	ln(L) = -1.648 + 1.621*ln(H)	LI	ln(V) = -3.717 + 2.437*ln(D)
CK-F	ln(L) = -2.257 + 1.621*ln(H)	GC-200	ln(V) = -0.085 + 1.235*ln(D)
WY-D8	ln(L) = -2.632 + 1.621*ln(H)	GC-725	ln(V) = -2.519 + 1.887*ln(D)
LI	ln(L) = -2.555 + 1.621*ln(H)		
GC-200	ln(L) = -2.376 + 1.621*ln(H)		
GC-725	ln(L) = -2.428 + 1.621*ln(H)		
Stem diameter v. crown length			
GO	ln(L) = -0.121 + 0.915*ln(D)		
LW-R6	ln(L) = -0.263 + 0.915*ln(D)		
LW-I6	ln(L) = -0.147 + 0.915*ln(D)		
WY-A	ln(L) = -0.642 + 0.915*ln(D)		
CK-B	ln(L) = -0.202 + 0.915*ln(D)		
CK-C	ln(L) = -0.240 + 0.915*ln(D)		
CK-N	ln(L) = -0.101 + 0.915*ln(D)		

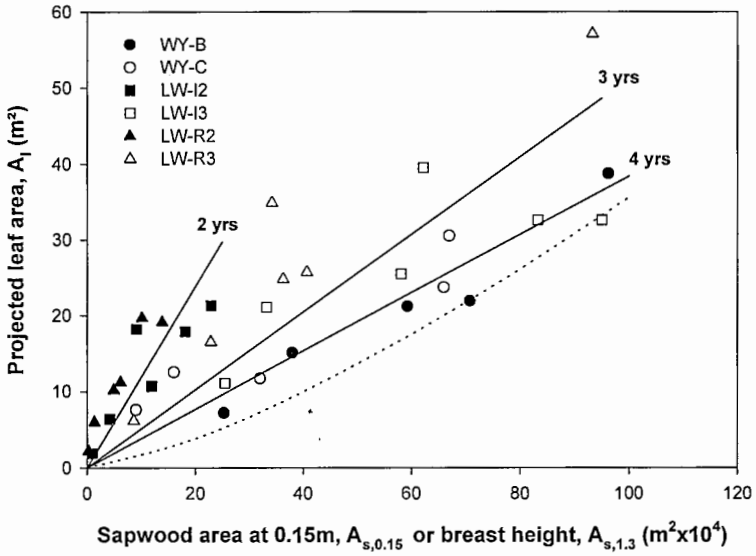


Figure 5.4 The relationship between sapwood area at breast height and leaf area for pre-canopy closure sites. Separate plots are shown for each site. Solid lines show change in relationship with age. Dotted line shows sapwood area - leaf area model for post-canopy closure trees (see equation 11).

For post-canopy closure sites, pooling of the data showed a strong non-linear relationship between both $A_{s,1.3}$ and $A_{s,cb}$ and the projected leaf area (A_l) of the tree across a sapwood area range of 7.0 - 340.3 cm^2. This relationship was stronger at crown base than at breast height (Figure 5.5a and b). Both relationships were site independent. The residuals from predicted A_l (transformed values) showed no bias in relation to A_s at breast height and crown base (Figure 5.6a and b). The calculated bias correction factors for back-transformation of the breast height and crown base models were 1.08 and 1.07 respectively. The individual models were;

$$A_l = 0.198 A_{s,cb}^{1.20} \quad (n=75, r^2=0.95) \quad 5.11$$

$$A_l = 0.059 A_{s,1.3}^{1.39} \quad (n=81, r^2=0.92) \quad 5.12$$

At a branch level, leaf area was strongly related to branch cross-sectional area (although the relationship varied with crown position and site - data not shown). Using these data we can also obtain a relationship between A_l of the canopy and $A_{s,br}$ for comparison with leaf area to stem sapwood cross-sectional area (recognising that leaf area was derived from branch cross-sectional area). This was reflected in a bias correction factor of 1.00, indicating no bias in the back-transformation of the logarithmic model.

$$A_l = 0.187 A_{s,br}^{1.08} \quad 5.13$$

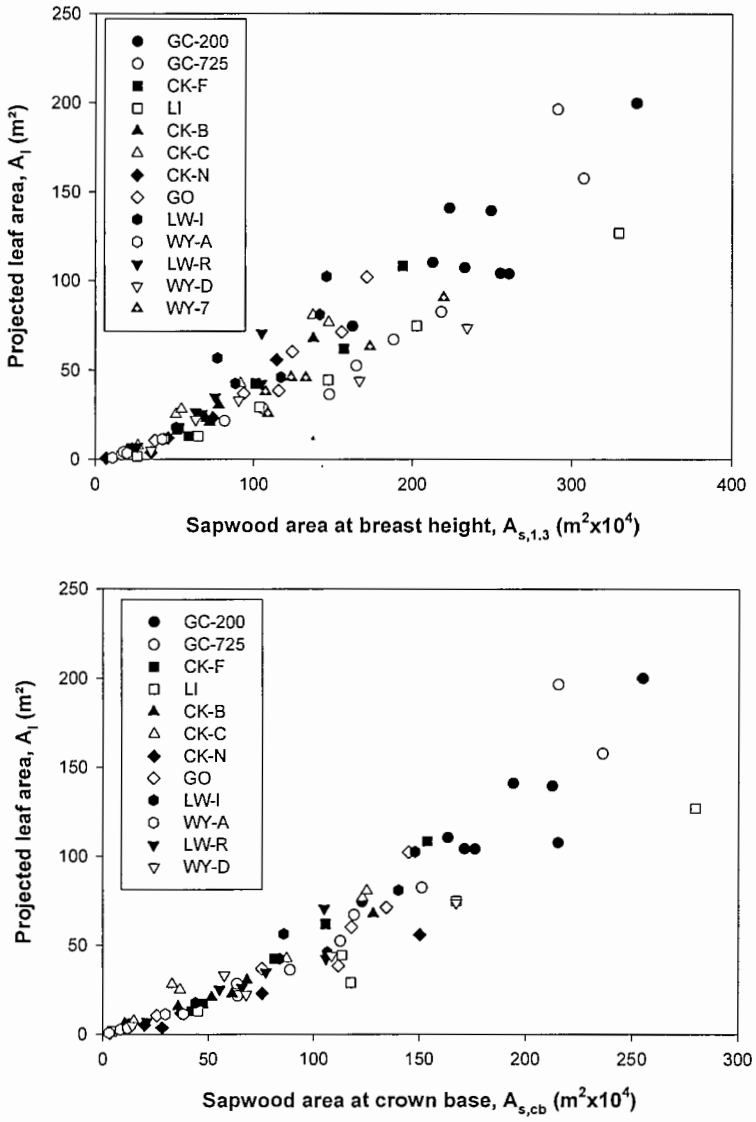


Figure 5.5 The relationship between (a) leaf area and sapwood area at breast height (n=81) and (b) leaf area and sapwood area at crown base (n=75) for post-canopy closure sites. Separate plots are shown for each site.

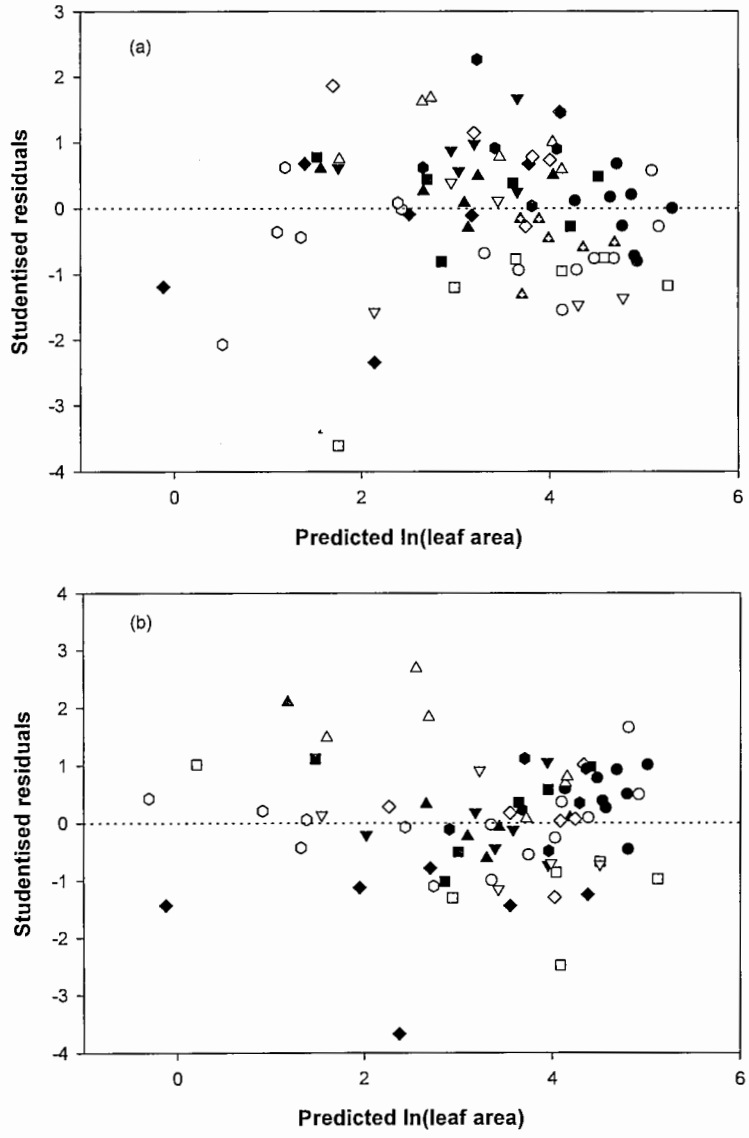


Figure 5.6 Studentised residuals (residual divided by standard error) from predicting leaf area from sapwood area at (a) breast height (Eq. 11) and (b) crown base (Eq. 12). Refer to Figure 5.5 for key to symbols.

5.3.3 Crown structure

5.3.3.a Specific leaf area

Specific leaf area (SLA) ranged from 1.43 to 8.30 $m^2 kg^{-1}$ for the sampled branches from post-canopy closure sites (n=1050). Overall mean SLA was 4.80 $m^2 kg^{-1}$. Mean SLA varied significantly across each of the three vertical crown zones and with tree age (Table 5.5).

Table 5.5 Mean specific leaf area (leaf area:leaf dry weight) of post-canopy closure trees for each of the three vertical crown zones. Letters indicate significant differences between tree age within each crown zone (α=0.05).

Age	SLA ($m^2 kg^{-1}$)
	Lower crown zone
6	5.29 a
7	4.94 b
8	4.87 bc
9	4.69 bc
13	4.58 c
	Middle crown zone
6	4.96 a
7	4.82 a
8	4.82 a
9	4.78 a
13	4.16 b
	Upper crown zone
6	4.92 b
7	4.99 b
8	4.75 b
9	5.50 a
13	4.02 c

5.3.3.b Crown length

The log-log relationship between crown length (L_c) and H_t followed a common slope across post-canopy closure sites, though intercepts were significantly different (n=75; r^2=0.94; Table 5.4). Likewise, the log-log relationship between L_c and $D_{1.3}$ had a common slope with varying intercepts (n=75; r^2=0.91; Table 5.4,

Figure 5.3b). A non-linear asymptotic model (West 1979) provided a good fit of the untransformed data pooled from both pre- and post-canopy closure sites.

$$L_c = \frac{D_{1.3}}{1.043 + (0.038 * D_{1.3})} \qquad (n=109, r^2=0.98) \qquad 5.14$$

L_c was shown to be a site-independent predictor of A_l for post-canopy closure sites with a back-transformation bias correction factor of 1.21.

$$A_l = 0.172 L_c^{2.38} \qquad (n=75, r^2=0.88) \qquad 5.15$$

5.3.3.c Branch length

Log-log analysis of branch diameter (D_{br}) and branch length (L_{br}) (n=1032) showed the relationship to be independent of crown zone but with significantly different slopes and intercepts across the post-canopy closure sites (r^2=0.96, Table 5.4).

5.3.3.d Leaf area density

Whole tree leaf area density ranged from 0.7 to 3.0 $m^2\ m^{-3}$ with a mean value of 1.6 $m^2\ m^{-3}$. Whole tree leaf area density increased with tree size but varied significantly between the four sites with CK-F and LI both significantly lower than GC-200 and GC-725 (Table 5.6). Mean leaf area density in each of the three crown zones varied by site (Table 5.6). Lowest leaf area densities were found in the lower third of the crown on each site. Maximum leaf area density was found in the middle crown zone at GC-200 and GC-725 and in the upper crown zone for CK-F and LI.

Table 5.6 Mean leaf area density ($m^2 m^{-3}$) of total crown and each crown zone for post-canopy closure sites with crown volume estimates. Letters indicate significant differences between sites within each crown zone (α=0.05)

Site	Mean leaf area density ($m^2 m^{-3}$)	S.E.
	Whole tree crown	
CK-F	1.31 b	0.15
LI	1.01 b	0.10
GC-200	1.91 a	0.06
GC-725	1.84 a	0.19
	Lower crown zone	
CK-F	1.17 a	0.15
LI	0.41 b	0.09
GC-200	1.30 a	0.16
GC-725	1.07 a	0.11
	Middle crown zone	
CK-F	1.37 b	0.17
LI	1.41 b	0.16
GC-200	2.65 a	0.23
GC-725	2.61 a	0.36
	Upper crown zone	
CK-F	1.62 a	0.28
LI	1.85 a	0.12
GC-200	1.33 a	0.11
GC-725	1.87 a	0.39

5.3.3.e Crown volume

Estimated crown volumes ranged from 2.3 to 113.5 m^3 and were correlated with $D_{1.3}$. Site influenced both the intercept and slope of the log-log relationship across the four post-canopy closure sites (n=28, r^2=0.97, Table 5.4).

5.4 Discussion

5.4.1 Stem relationships

Consistent with the findings of Chapter 4, a constant taper was found between $A_{s,1.3}$ and $A_{s,cb}$ in post-canopy closure trees across a range of sites. The reduction in sapwood area in *E. nitens* was independent of site and suggests a redundancy of sapwood vessels at lower stem heights and/or a change in sapwood hydraulic

conductivity with height. While sapwood conductivity was not measured at each site, the conductivity of sapwood has been shown to increase with height (Chapter 4, Shelburne and Hedden 1996). Given the constant ratio between $A_{s,1.3}$ and $A_{s,cb}$, it was expected that the relationship between $A_{s,cb}$ and total $A_{s,br}$ would also be linear. This relationship, while strong, was found to be curvilinear. Branch sapwood area was not measured directly in this study and the cross-sectional area of branches at the stem was assumed to be composed entirely of sapwood. However, large branches on older trees were likely to have heartwood present and this would have contributed to the non-linear nature of this relationship.

The change in H_t with $D_{1.3}$ in this study was rapid in smaller trees and slower for larger trees. Empirically, the observed relationship can be described with a rectangular hyperbola where height approaches an asymptotic maximum with increasing diameter (Causton 1985). A form of this relationship used by West (1979) provided a good fit to the data of this study. This change can be viewed in terms of mechanical support requirements to ensure stability. The stem of a tree must be strong enough to support the static load of the tree's own biomass in addition to the dynamic loading of wind (to which the crown provides the majority of resistance). The observed decrease in height growth with increasing tree size and age can also be viewed in terms of physiological limitations associated with the maintenance cost of sapwood (Mäkelä 1986).

5.4.2 Leaf area - sapwood area relationships

Examination of a variety of allometric relationships for *E. nitens* found that a number were stable across sites subject to markedly different silviculture and environmental conditions. The most notable was that between projected leaf area and sapwood cross-sectional area. At approximately 4 years of age, the point of

canopy closure for many of these stands, the relationship became stable. As trees aged between 2 and 4 years, there was a marked decrease in the amount of leaf area per unit sapwood area. Owing to limited sampling across sites, site effects could not be totally excluded. However, the pre-canopy closure sample included trees at ages 2 and 3 years from the same site (LW), suggesting a real age effect. The period of time leading up to canopy closure is characterised by changes in the relative partitioning of biomass between leaves and stem (Beadle and Inions 1990). This change may be induced by the rapidly-changing light conditions experienced by individual crowns within the stand. Beadle and Mummery (1989) reported a similar decrease to that reported here in the ratio of leaf area to sapwood area in two provenances of *E. nitens* between ages 1 and 4 years. This decrease was matched with a change in carbon allocation from leaf mass to stemwood. The authors noted that the relationship was approaching stability as the stands reached canopy closure. It is also observed that at canopy closure the crowns of eucalypt trees rise rapidly and extensive litterfall occurs. Such an event will alter the A_l - A_s relationship in the short-term.

In post-canopy closure trees, the leaf area - sapwood area relationship was stronger (and more linear) at crown base compared with breast height. The non-linear nature of the relationship between $A_{s,1.3 \text{ or } cb}$ and A_l contradicts other reports of a constant A_l - A_s ratio (eg. Robichaud and Methven 1992). The power value of greater than unity in equations 5.11 and 5.12 indicates that as tree sapwood cross-sectional area gets larger, more leaf area is produced per unit increase in sapwood cross-sectional area. However, examination of the data does not indicate that this is a result of the dominance class of individual trees in the stand and given that tree size varies across all of the stands it is unlikely to be a result of site-related

differences. The increase in sapwood permeability with age (Pothier et al. 1989) can provide some explanation for the change in the A_l - A_s relationship with A_s. Further to this, the tendency of sapwood permeability to increase with age more rapidly on better quality sites (Pothier et al. 1989) possibly provides an explanation for higher A_l - A_s ratios in better quality sites compared with poorer sites of the same age in this study.

5.4.3 Crown structure

Mean SLA was greatest in the lower crown zone and least in the upper crown zone. This pattern may be linked to available light levels (Bartelink 1997; Gratani 1997) where a higher mean SLA in lower reaches of the crown is a morphological response to reduced light availability with less carbon invested per unit light intercepted (Beadle 1993).

While SLA did vary between sites in this study, there was no consistent pattern across all sites. WY-A, a low quality site, showed significantly lower SLA in each crown zone compared with higher quality sites of the same age. Irrigated trees at the LW site had significantly higher SLA than rain-fed trees in each of the crown zones, supporting earlier studies which found that mean SLA decreased with decreasing annual rainfall in *Eucalyptus* species (Mooney et al. 1978; Bennett et al. 1997) and other tree species (Jose and Gillespie 1997).

The relationship between L_c and $D_{1.3}$ held only for post-canopy closure sites and was similar in form to the relationship between H_t and $D_{1.3}$. Prior to canopy closure the L_c of individual trees is not limited by light and the relationship between tree size ($D_{1.3}$) and L_c is less pronounced. Canopy closure is characterised by a reduction in light levels reaching the base of the crown which results in death

of foliage and subsequent canopy 'lift'. The degree of impact that canopy lift has on the L_c of tall individual trees will be less than that of smaller trees of the same age.

Leaf area densities in this study were considerably higher than other values for eucalypt forest. For example Pook (1984) found a mean leaf area density of 0.23 $m^2 m^{-3}$ for a 16 year-old *E. maculata* stand. However, the estimate of Pook (1984) appears to be based on plot volume, whereas for this study, leaf area density was based on individual crown volume. For the sites where crown volume was estimated, whole tree leaf area density was significantly higher in older stands (GC) compared with younger stands (CK-F and LI). It was notable that whole tree leaf density did not differ between the thinned and unthinned stands at GC. The higher (but not significant) leaf area density in the lower crown zone of GC-200 compared with GC-725 is possibly indicative of foliage being retained in this zone due to the improvement of light availability following thinning. While thinning can be expected to produce a downward shift in relative leaf distribution (Maguire and Bennett 1996) it appears that the change in crown volume results in little change in leaf area density. The older stands (GC) had the greatest leaf area density in the middle crown zone while the leaf area density of younger stands (CK-F and LI) was found in the upper crown zone. With the data available it was impossible to determine if this was an age effect or simply due to site differences.

5.5 Conclusions

The allometric relationships established for *E. nitens* have a number of potentially useful applications. Leaf area is a fundamental variable in predicting photosynthesis, transpiration and respiration in forest stands. These processes

form the background for the reported correlation between light interception and stand productivity (Waring 1983; Linder et al. 1985). The stability of the sapwood area and leaf area relationships means they can be applied in the indirect estimation of leaf area index (L) for *E. nitens* plantations. This has been done with other tree species (Marshall and Waring 1986; Whitford et al. 1995; Pereira et al. 1997). Furthermore, the allometric relationships have potential for incorporation into a process-based growth model for *E. nitens*. These empirical relationships can determine biomass partitioning or carbon allocation within trees in terms of tree size (Mäkelä 1986; Landsberg and Waring 1997).

While the relationships have been established using plantations from across Tasmania, their use outside this geographic region is not recommended without local validation. Changes in the leaf area - sapwood area relationship with climate have been reported for other tree species. Mencuccini and Grace (1995) found a decrease in the leaf area - sapwood area ratio of *P. sylvestris* trees with increasing average vapour pressure deficit (VPD). Across Tasmania, the range of average VPD is small and the impact of warmer, drier climates on leaf area - sapwood area relationships in *E. nitens* can only be speculated upon at this stage.

Equations 5.11 and 5.12 describe the relationship between sapwood area and leaf area in *E. nitens* but provide no description of the arrangement of the leaf area within the crown. In the following chapter, the effect of thinning on crown architecture is examined and its effect on productivity considered.

Chapter 6. Crown structure and leaf area index development

6.1 Introduction

Canopy size determines the productivity of forest stands through its role in radiation interception. Size is often measured as the leaf area index and this variable plays a key role in interception models (Jarvis and Leverenz 1983; Landsberg and Hingston 1996). Further, the structure of the crowns of individual trees also plays an important role in stand production through its effect on the penetration of light (Kellomäki et al. 1985) and canopy microclimate, including temperature, vapour pressure deficit and windspeed (Gary 1974). An understanding of both canopy size and structure is required to better understand and model growth.

Growth models in which radiation absorption is calculated on a stand basis commonly employ a horizontally continuous canopy of a given leaf area index (eg. Linder et al. 1985; Landsberg and Hingston 1996). While this approach is satisfactory for a closed canopy, it is less suitable for stands with a discontinuous or clumped canopy (eg. thinned stands). A theoretical consideration of the influence of canopy structure using Beer's law to describe light extinction throughout tree canopies showed that leaf area distribution can have an important effect on the amount of light absorbed (Larsen and Kernshaw Jr. 1996). Differences in canopy structure such as canopy depth and foliar density across a range of even-aged *P. contorta* stands were found to directly influence the amount and efficiency of stemwood production (Smith and Long 1989). Thus, the value in

incorporating measures of foliage distribution into models of carbon gain has been recognised (McMurtrie et al. 1986; Whitehead 1986; Wang and Jarvis 1990; Whitehead et al. 1990).

High intensity thinning as practised in *E. nitens* plantations in Tasmania can change stand leaf area index dramatically. It is also likely that the discontinuous canopy resulting from thinning will affect levels of available radiation for individual trees and potentially alter the structure of tree crowns and that of the stand as a whole. Changes in vertical distribution of foliage with stand density or following thinning have been found in other tree species. Heavily thinned *P. radiata* trees had a greater proportion of their foliage in lower sections of the crown than lightly thinned trees because of greater branch size and number (Siemon et al. 1980). An improvement in light conditions in the lower crowns of 24 year-old *P. menziesii* after thinning resulted in an increase in the foliage area of lower crown whorls after seven years (Brix 1981). Similarly, wider spacing induced a downward shift in relative foliage distribution in *P. menziesii*, with the effect more pronounced with increasing tree dominance (Maguire and Bennett 1996). However, some studies have found no difference in foliage distribution with thinning or stand density. A 'normal' distribution of foliage was found for *Pinus resinosa* (Ait.) trees and stands despite differences in tree size and age, stand density and site quality (Stephens 1969). No effect of thinning or fertilization was found on the vertical distribution of foliage in *P. taeda* (Gillespie et al. 1994).

While the vertical distribution of foliage is known to vary widely between non-coniferous tree species (Jarvis and Leverenz 1983), few studies have been carried out on the vertical distribution of foliage in *Eucalyptus* stands. One study in a

regenerating stand of *Eucalyptus maculata* Hook. found the vertical distribution of leaf area was skewed to the top of individual tree crowns (Pook 1984). In a coppiced plantation of *E. globulus* the maximum amount of leaf area was found near the mid-point of the live crown (Pereira et al. 1987).

The objectives of the present study were to; (i) characterise the crown structure and vertical distribution of leaf area for mid-rotation (10 to 15 year-old) *E. nitens* plantations, (ii) determine the effect of thinning on crown structure and vertical distribution of leaf area and (iii) quantify the rate of recovery of canopy leaf area following thinning.

6.2 Materials and Methods

6.2.1 Crown structure

Detailed crown measurements were made at the Goulds Country thinning trial. Measurements of stand leaf area index were made at each of the three thinning trials described in Chapter 2.

Measurements of crown structure were carried out on sixteen trees destructively sampled from Goulds Country as described in Chapter 4. In addition to diameter, the height of emergence on the main stem was also measured for each branch. The branch angle from the main stem was measured to the nearest five degrees, and the azimuth sector of each branch was also recorded as either 1 (north to east), 2 (east to south), 3 (south to west), or 4 (west to north). Destructive sampling was carried out during the winter of 1997. A sub-sample of five branches was selected from each of the three crown zones, representing the range of branch diameters present in the zone. Each of the sample branches was measured for total length. The leaf area of each branch was determined as described in Chapter 4.

Linear regression was used to derive relationships predicting branch leaf area and branch length from branch cross-sectional area. The relationships were applied to the measured diameter to calculate the leaf area and length of branches that were not sampled.

Assuming no curvature along the branch length, the stem height at which each branch tip occurred (H_x) was estimated using:

$$H_x = H_0 + \cos\theta \times L_{br} \qquad 6.1$$

where H_0 was height of branch emergence, θ was branch angle from the vertical and L_{br} was branch length. The leaf area of each branch was distributed evenly between H_0 and H_x using 0.1 m height intervals. The crown length of each tree was divided into 0.1 m sections and branch leaf area within each section was summed and expressed as a proportion of total leaf area. These data were fitted to a two-parameter cumulative Weibull function using the NLIN procedure in SAS (SAS Institute Incorporated 1990) to analyse the vertical distribution of foliage. The cumulative distribution function took the form:

$$LA_c = 1 - \exp[-(RH/\beta)^{\alpha}]/1 - \exp[-(1/\beta)^{\alpha}] \qquad 6.2$$

where LA_c is the cumulative proportion of leaf area, RH is relative crown height, and α and β are estimated parameters. The equation was normalised by the denominator term. The α parameter in Equation 2 describes the shape of the distribution. For $1<\alpha<3.6$ the probability distribution is mound shaped and positively skewed, if $\alpha = 3.6$ the distribution is approximately normal, and if $\alpha >$ 3.6 the distribution becomes negatively skewed (*ie.* more foliage towards lower sections of the crown) (Bailey and Dell 1973). The β parameter describes the

scale of the distribution and has been interpreted as leaf area density or leaf area per unit height (Gillespie et al. 1994).

The fitted Weibull function was used to estimate the proportion of leaf area at a given crown location:

$$LA_x = LA\{\exp[-(x-w)/\beta]^{\alpha} - \exp[-(x+w)/\beta]^{\alpha}\}/1-\exp[-(1/\beta)^{\alpha}] \qquad 6.3$$

With total tree leaf area (LA), the predicted leaf area (LA_x) within an interval of crown length having midpoint x and width $2w$ can be estimated using Equation 6.3.

Crown volume was estimated by calculating the horizontal projection length of each branch at its maximum stem height, H_x. The stem height at which the maximum branch projection length occurred was identified. Thus the crown volume was estimated by summing the volume of two half-ellipsoids, each with a base area equal to the maximum crown projection area of the tree. The stem height at which the lowest green branch emerged defined the base of the lower ellipsoid.

Leaf area density (LAD) of each tree was calculated as the ratio of total leaf area to estimated total crown volume.

6.2.2 Leaf area index - stand measurement

Measurements of leaf area index (L) were made at Goulds Country, Lisle and Creekton using a LAI-2000 Plant Canopy Analyser (PCA) (Li-Cor Inc., Lincoln, Nebraska, USA). Readings were taken either during uniform, diffuse light conditions with 100 per cent cloud cover, or during dawn and dusk. Three readings were taken from the four corners of each plot with a 270° viewcap to limit the reading to the plot. Understorey exceeding 1.5 m in height was cleared to

a distance of approximately 5 m from each plot corner. A sensor was set up outside the plantation to continuously record light conditions. The sensor outside the plantation (also with 270° viewcap) was rotated to take readings in the same direction as each of the readings inside the plantation.

Plot measurements of L at Lisle and Creekton were made six months and 18 months after thinning. Plot measurements of L at Goulds Country were carried out during March 1997, seven years after thinning (*i.e.* when the plantation was 13 years old). In each instance, output from the PCA was converted to a L value using a calibration factor developed for plantation *E. nitens* in Tasmania (Cherry et al. 1998). The outer ring of the PCA was excluded from the L calculation to ensure that the reading was constrained to the plot. Thick understorey in the Goulds Country trial meant limiting measurements to one plot per thinning treatment. A regression of L to stand basal area was used to estimate L of the remaining plots. At Goulds Country, L immediately after thinning at age 6 years was estimated using an allometric relationship between tree size and tree leaf area (see Chapter 5, equation 5.12) and known tree sizes recorded at the time of thinning. The change in mean crown length at Goulds Country was calculated using crown lengths measured at age 7 and 13 years. Crown length was measured from a sub-sample of 100 trees ha^{-1} in each plot. The change in leaf area per tree was calculated from L estimates at age 6 and measurements at 13 years.

6.2.3 Leaf area index - isolated tree measurement

The wide spacing and relatively small crowns of the 100 trees ha^{-1} treatment at Lisle and Creekton meant that the plot corner method presented difficulties. If the below-canopy reading is close to that of the above-canopy reading, the reading will be rejected by the PCA (LI-COR 1990). To overcome this, a single-tree

sampling method was tested at Creekton. In this method L is calculated from crown projection area using the PCA measurement of LAD. LAD is calculated by the PCA using a set of x,y coordinates which describe crown shape and hence the length of crown 'seen' by each of the five concentric rings. The crowns of trees at Creekton were assumed to be ellipsoids, meaning measurements of height to crown base, crown length and crown width were required to determine the x,y coordinates for each of the PCA five viewing angles (Figure 6.1, after Acock et al. 1994). Measurements of LAD of isolated trees were carried out at Creekton on 24 March 1998. In the 100 trees ha^{-1} plots, a reading was taken at the base of each tree in each of the north, south, east and west directions (using a 180° viewing cap to obscure operator and tree stem). This was replicated three times. Total height, height to crown base and crown width in each of the four directions was measured for each tree.

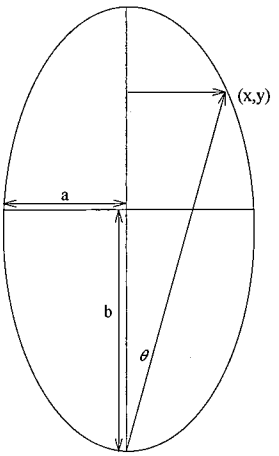


Figure 6.1 Diagram showing distance from crown base to edge of tree crown at (x, y) assuming ellipsoid shape of crown. Where a is 0.5 crown width and b is 0.5 crown height and where $y = 2a^2b / (b^2\tan^2\theta + a^2)$ and $x = y(\tan\theta)$ (reproduced from Acock et al. 1994).

Distances from crown base to the edge of the crown were calculated for each tree

using the five angles of the PCA (7, 23, 38, 53 and 68°) and the assumptions of crown shape as described in Figure 6.1. A L for the tree was obtained by only using the fields of view of the PCA which fell within the lateral extension of the crown.

A leaf area estimate for each tree was obtained using the measurements of LAD and crown volume calculated by the PCA. This was compared with leaf area estimated using tree diameter measurements from 12 months prior to the PCA measurements and the relationship for *E. nitens* between tree size and leaf area described in Chapter 5 (Equation 5.12).

6.2.4 Data analysis

Branch cross-sectional area (at 40 mm from the stem, A_{br}), branch length (L_{br}) and branch leaf area ($A_{l,br}$) data were transformed using natural logarithms. A group linear regression procedure was used to determine the significance of thinning treatment and crown zone on relationships between the branch cross-sectional area, branch leaf area and branch length data. Correction coefficients for back-transformation bias in logarithmic models were calculated using the method of Snowdon (1991). Differences in specific leaf area (SLA) between treatments and crown zones were tested with analysis of variance.

Differences in branch arrangement between thinning treatments were analysed using unpaired t-tests while differences within trees were analysed using paired t-tests. The change in stand leaf area index at Lisle and Creekton was analysed using regression analysis.

6.3 Results

6.3.1 Branch structure

The relationship between branch cross-sectional area (A_{br}) and branch length (L_{br}) was independent of thinning treatment ($p > 0.05$). However, the slope and the intercept were influenced by crown zone ($p < 0.05$, Table 6.1). There was little overlap in A_{br} values between crown zones. In the upper zone, 75 per cent of branches were less than 11 mm in diameter while only 25 per cent of branches in the lower zone were less than 30 mm and the smallest branch diameter measured in the lower zone was 18 mm. The correction coefficient for back-transformation bias of the logarithmic model was 1.05.

Table 6.1 Values of parameters for a linear regression model to predict the natural logarithm of branchlength (L_{br}) as a function of the natural logarithm of branch cross-sectional area (A_{br}) by crown zone (i), $\ln(L_{br})_i = (\bar{a} + a_i) + (\bar{b} + b_i)\ln(A_{br})$, for thinned and unthinned trees at Goulds Country. Standard errors of parameters are in parentheses. The coefficient of determination (r^2) for the model was 0.95.

Parameter	Effect	Details	Parameter value
Intercept	Mean ($\bar{a}$)		-1.69 (0.06)
	Zone (a_i)	i=lower zone	0.41 (0.16)
		i=middle zone	0.14 (0.09)
		i=upper zone	0.00
Slope	Mean ($\bar{b}$)		0.43 (0.01)
	Zone (b_i)	i=lower zone	-0.07 (0.02)
		i=middle zone	-0.04 (0.02)
		i=upper zone	0.00

There was a common slope across thinning treatments and canopy zones for the relationship between A_{br} and branch leaf area ($A_{l,br}$). However, while the intercept of the relationship was common between branches from thinned and unthinned trees, it was necessary to use a different intercept for each canopy zone ($p < 0.01$, Table 6.2). The branches of the lower zone had the lowest intercept, so when the

model was back-transformed, branches in this zone had a smaller leaf area for a given branch cross-sectional area compared with the other crown zones. The correction coefficient for back-transformation bias of the logarithmic model was 1.08.

Table 6.2 Values of parameters for a linear regression model of the natural logarithm of branch leaf area ($A_{l,br}$) as a function of the natural logarithm of branch cross-sectional area (A_{br}) by crown zone (i), $\ln(A_{l,br})_i = (\bar{a} + a_i) + \bar{b}\ln(A_{br})$, for thinned and unthinned trees at Goulds Country. Standard errors of parameters are in parentheses. The coefficient of determination (r^2) for the model was 0.91.

Parameter	Effect	Details	Parameter value
Intercept	Mean ($\bar{a}$)		-7.06 (0.15)
	Zone (a_i)	i=lower zone	-0.61 (0.10)
		i=middle zone	0.20 (0.09)
		i=upper zone	0.00
Slope	Mean ($\bar{b}$)		1.18 (0.03)

The proportion of branches in each crown zone of thinned and unthinned trees was similar ($p > 0.05$). On average, 16 per cent of branches were found in the lower third of the crown, 32 per cent in the middle crown, and 52 per cent in the upper crown zone. Consequently, the branching density of each crown zone was similar for thinned and unthinned trees ($p > 0.05$) with an average of 2.9 branches m^{-1} of stem height in the lower, 5.8 branches m^{-1} in the middle, and 9.4 branches m^{-1} in the upper zone.

Significantly larger branches were found in the lower crown zone of thinned trees when compared with unthinned trees ($p < 0.05$). Similar branch sizes were found in the middle and upper crown zones across thinning treatments.

A similar proportion of branches was found on the northern (51%) and southern (49%) aspects of thinned and unthinned trees ($p > 0.05$). The branches on the

northern aspect of thinned trees were significantly larger than the branches on the southern aspect ($p < 0.01$) while no significant difference was found between branch sizes of northern and southern aspects in unthinned trees ($p > 0.05$).

Branch angle from the vertical increased with crown depth. Mean branch angle was positively correlated to tree diameter at breast height in the lower and middle crown zones ($p < 0.01$, Figure 6.2c,b), but no relationship was found for the branches in the upper crowns ($p > 0.05$, Figure 6.2a). Thinning did not significantly affect mean branch angle in any of the three crown zones ($p > 0.05$).

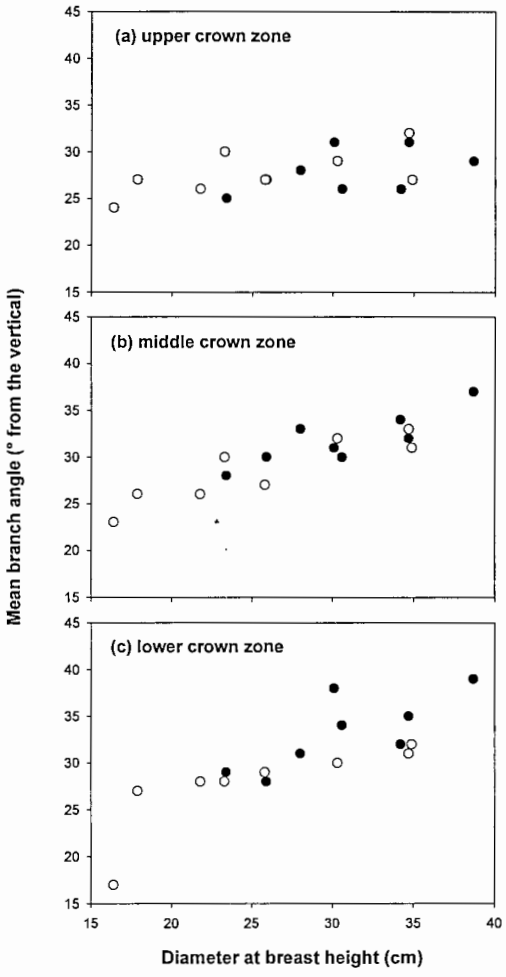


Figure 6.2 Mean branch angle from the vertical by tree diameter for (a) upper crown zone, (b) middle crown zone, and (c) lower crown zone. Closed symbols are thinned trees, open symbols are unthinned trees.

6.3.2 Within-tree leaf area distribution

Thinned and unthinned trees had similar amounts of leaf area in each of the lower, middle and upper crown zones in the southern aspect ($p > 0.05$). In the northern aspect, thinned trees had greater amounts of foliage in the lower and middle

crown zones ($p < 0.05$, Figure 6.3a-d). Specific leaf area (SLA) decreased with increasing crown height ($p < 0.01$) but no significant difference was found between the thinning treatments ($p = 0.06$).

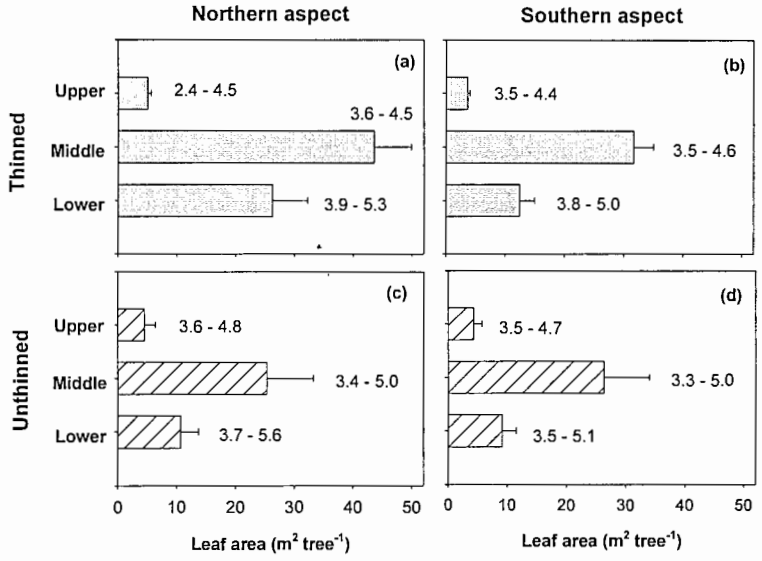


Figure 6.3 Leaf area histograms (m^2 $tree^{-1}$) and range of specific leaf area data values (m^2 kg^{-1}) for the upper, middle and lower parts of the crown of thinned (a and b) and unthinned (c and d) trees. Charts (a) and (c) show the northern aspect of the crown, charts (b) and (d) show the southern aspect. Error bars show the mean standard error.

The Weibull model provided an adequate fit of the vertical leaf area distributions for both thinned and unthinned trees (Figure 6.4a,b). The α parameter was correlated with tree size in the unthinned treatment, with smaller trees having more foliage towards the top of the crown (Table 6.3). The α parameter showed no clear relationship with tree size in the thinned treatment. A strong relationship

between the live crown ratio (ratio of green crown length to total tree height) and α was found for unthinned trees (Figure 6.5).

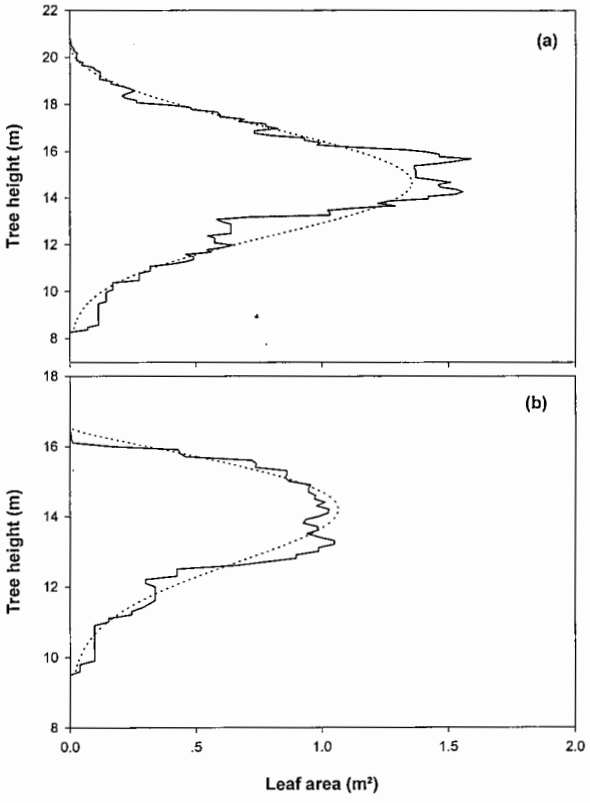


Figure 6.4 Examples of vertical leaf area distribution for (a) thinned and (b) unthinned trees at Goulds Country. Dotted lines show fitted Weibull function.

Table 6.3 Weibull parameter estimates for crown leaf area distribution by thinning treatment. 95% confidence intervals are shown in parentheses.

Treatment	DBH (cm)	α	β
thinned	23.4	3.195 (3.144-3.245)	0.545 (0.543-0.547)
	25.9	2.628 (2.608-2.648)	0.571 (0.570-0.573)
	28.0	2.710 (2.680-2.740)	0.479 (0.478-0.480)
	30.1	2.709 (2.693-2.726)	0.564 (0.563-0.565)
	30.6	3.024 (2.997-3.052)	0.492 (0.491-0.494)
	34.7	2.274 (2.250-2.297)	0.477 (0.475-0.478)
	34.2	2.511 (2.492-2.530)	0.539 (0.538-0.540)
	38.7	2.473 (2.442-2.504)	0.553 (0.551-0.555)
unthinned	16.4	2.441 (2.400-2.483)	0.558 (0.556-0.561)
	17.9	2.012 (1.964-2.059)	0.458 (0.455-0.462)
	21.8	2.159 (2.134-2.183)	0.445 (0.444-0.447)
	23.3	2.477 (2.446-2.507)	0.461 (0.460-0.463)
	25.8	2.651 (2.633-2.670)	0.540 (0.539-0.541)
	30.3	2.718 (2.696-2.741)	0.487 (0.486-0.488)
	34.7	2.554 (2.527-2.582)	0.485 (0.483-0.486)
	34.9	2.832 (2.809-2.854)	0.528 (0.527-0.529)

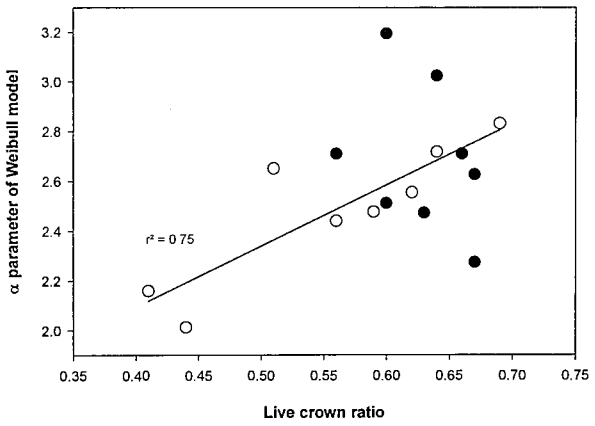


Figure 6.5 Relationship between live crown ratio and the α parameter of the Weibull function (shape of the vertical foliage distribution) for thinned and unthinned trees at Goulds Country. Closed symbols are thinned trees and open symbols are unthinned trees. The regression line is fitted only to the unthinned data.

The assumptions about crown shape provided a reasonable estimate of crown volume (Figure 6.6a,b). Tree leaf area density (LAD) was independent of tree size. The mean LAD of thinned trees was 0.91 $m^2 m^{-3}$ while the mean LAD of unthinned trees was 1.04 $m^2 m^{-3}$. This difference was not statistically significant ($p > 0.05$, *t*-test).

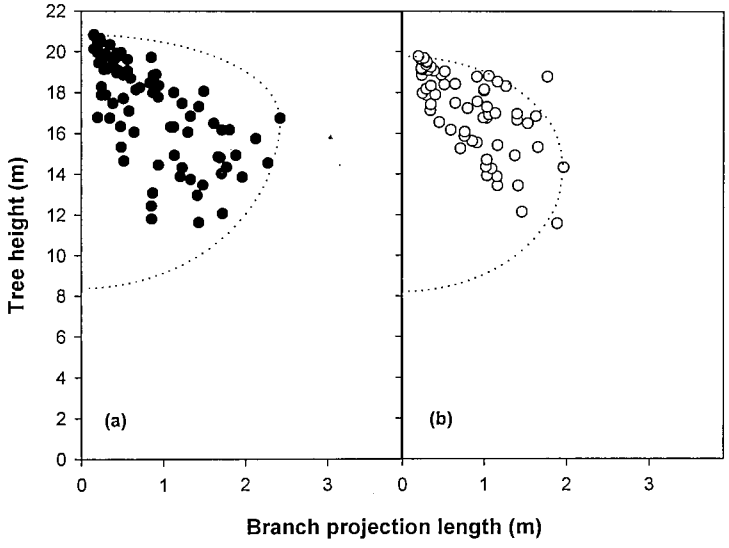


Figure 6.6 Examples of crown shape using the height of each branch tip and its horizontal projection length to define crown projection area with stem height for (a) a thinned (●), and (b) an unthinned (○) tree at Goulds Country. Dotted lines show the maximum crown width predicted at each height using the ellipsoid model described in the Materials and Methods section.

6.3.3 Leaf area index - stand measurement

Values for leaf area index (*L*) increased at a similar rate for all thinning treatments at Lisle during the first 18 months post-thinning (Table 6.4). *L* of the unthinned treatment did not change during this period. Each thinned treatment increased *L*

by approximately 0.5 m^2 m^{-2} during the 6 - 18 months post-thinning. At Creekton, L increased in the 18 months post-thinning in the 250 trees ha^{-1}, the 600 trees ha^{-1} and the unthinned treatments. The L of the 100 trees ha^{-1} treatment did not change during this period (Table 6.4).

Table 6.4 Leaf area index (L) by thinning treatment six and 18 months post-thinning at Lisle and Creekton. Numbers in brackets are standard deviations.

Treatment (residual stocking)	L 6 months post-thin	L 18 months post-thin
Lisle		
100 trees ha^{-1}	0.28 (0.20)	0.82 (0.14)
250 trees ha^{-1}	1.04 (0.36)	1.60 (0.14)
600 trees ha^{-1}	2.23 (0.23)	2.78 (0.02)
unthinned	4.05 (0.44)	4.25 (0.40)
Creekton		
100 trees ha^{-1}	0.65 (0.17)	0.52 (0.19)
250 trees ha^{-1}	0.95 (0.10)	1.51 (0.39)
600 trees ha^{-1}	2.11 (0.13)	2.91 (0.32)
unthinned	3.99 (0.27)	4.87 (0.31)

At Goulds Country, L varied with stocking level ($p < 0.01$) (Figure 6.7a). Six years after thinning (*i.e.* at age 13 years), L increased with stocking from 1.47 (100 trees ha^{-1}) to 4.32 in the unthinned treatment (725 trees ha^{-1}). The percentage increase in L after thinning declined with increasing residual stocking from 220% for the 100 trees ha^{-1} treatment to 117% for the unthinned treatment. The change in leaf area per tree was strongly related to the intensity of thinning (Figure 6.7b).

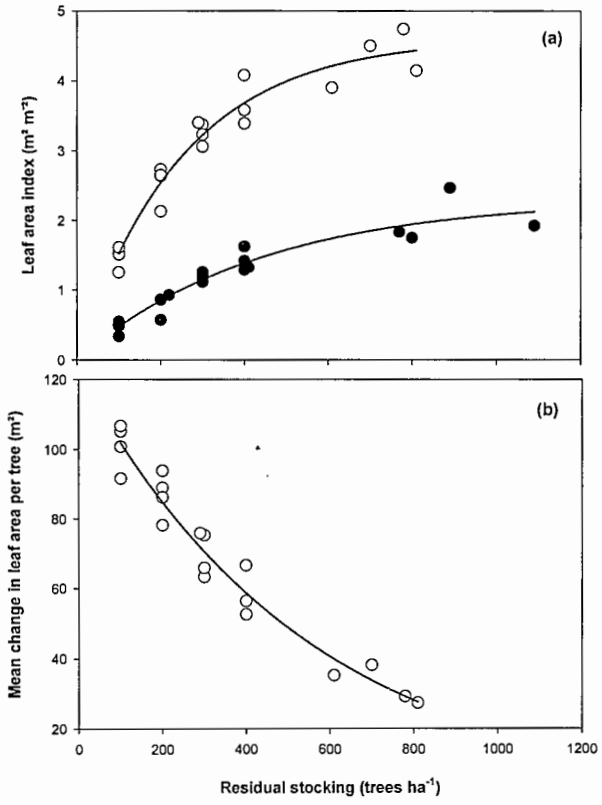


Figure 6.7 (a) Leaf area indices at thinning (●) and seven years after thinning (○) at Goulds Country. Curves show line of best fit at thinning, *y=2.32[1-exp(-0.002x)]* (r^2=0.91) and seven years after thinning, *y=4.61[1-exp(-0.004x)]* (r^2=0.95). (b) Mean change in leaf area per tree from age 6 to 13 years by residual stocking at Goulds Country. The curve shows the line of best fit, *y=122.54[exp(-0.002x)]* (r^2=0.95).

The change in leaf area per tree in the thinned treatments was associated with an increase in crown length (Figure 6.8). The change in leaf area per tree in the unthinned treatment was less strongly related to change in crown length.

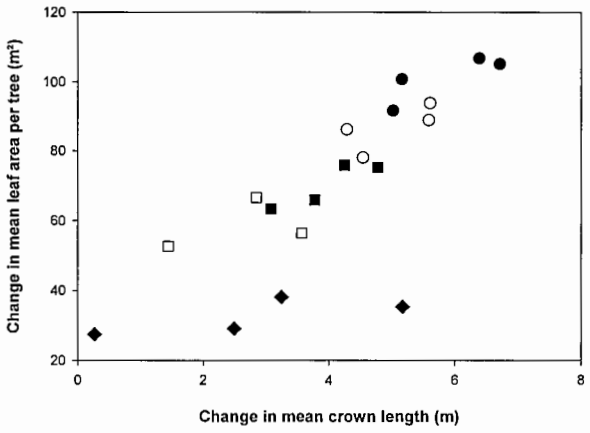


Figure 6.8 Change in leaf area per tree with crown length by thinning treatment at Goulds Country. (●=100 trees ha^{-1}, ○=200 trees ha^{-1}, ■=300 trees ha^{-1}, ❑=400 trees ha^{-1}, ◆=unthinned)

6.3.4 Leaf area index - isolated tree measurement

Out of 24 trees measured at Creekton in the 100 trees ha^{-1} treatment, only one tree had a crown base low enough (4.1 m) so that two rings (7° and 23°) could be used to calculate leaf area. This was the only tree to have an estimated leaf area greater than that calculated for 12 months previously using allometric relationships between stem size and leaf area (Figure 6.9). The height to crown base measures of the remaining trees were all greater than 4.1 m and the PCA calculation of LAD was confined to measurements made using only the 7° ring. The use of isolated tree measurements in *E. nitens* stands of low stocking was considered to produce an underestimate of stand L and hence the plot corner method was the preferred method for estimating L.

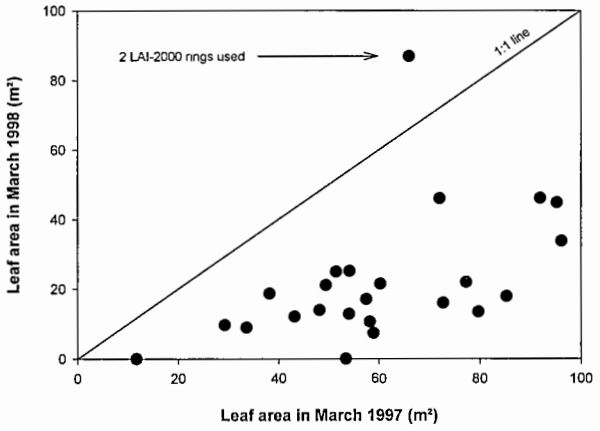


Figure 6.9 Comparison of individual tree leaf area estimates in the 100 trees ha^{-1} treatment plots at Creekton. Estimates for March 1997 were based on allometric relationships between stem diameter and leaf area established from destructive sampling. Estimates for March 1998 were from individual tree measurement of leaf area using the Li-cor LAI-2000 PCA. Note single tree above the 1:1 line where two detector rings of the PCA were able to be used. Remaining trees used a single detector ring (7°) only.

6.4 Discussion

6.4.1 Branching structure

This study has shown that branch size and hence crown size can be manipulated through thinning treatment. However the basic elements of crown structure such as branching density, angle and orientation were unaffected by thinning. The environment in which a tree grows can affect branch properties. For example, large differences in branch angle were noted between open-grown and shaded trees for a number of Tasmanian rainforest species including *Nothofagus cunninghamii* (Hook.) Oerst. and *Atherosperma moschatum* Labill. (King 1998). Such differences are likely due to the ability of shade-tolerant species to alter branching pattern in response to light levels to maximise light interception. It is

possible that shade-intolerant species such as *E. nitens* (Boland et al. 1984) have less plasticity in branching structure and branch morphology is more an expression of genotype (Colin et al. 1993).

The decrease in branching density with crown depth can be attributed to the within-crown light distribution and competition between branches during crown development and their displacement into lower parts of the crown. Changes in the form of branches with increasing size reflects the structural support requirements of each branch (Ford 1985). In this study, changes in form were evident by the exponential increase in branch leaf area (Table 6.2) and a slowing of the rate of increase in branch length (Table 6.1) with branch cross-sectional area. In addition, the increase in branch angle from the vertical with crown depth may be driven by branch load due to increase in wood and leaf biomass with branch size. The increase in mean branch angle with tree size in the middle and lower crown zones supports this, as larger branches were associated with larger stems (data not shown). An increase in branch angle from the vertical with crown depth may also assist in maximising effective leaf area display for light interception by reducing self-shading (Hutchinson et al. 1986; Hollinger 1989). The statistical differences in the relationship between A_{br} and L_{br} with crown zone may be due to its strongly non-linear nature and little overlap in A_{br} values between crown zones.

The change in tree leaf area with thinning was due to the subsequent growth of larger branches in the lower section of the crown. The improved light conditions in this section of the crown after thinning are likely to have induced the greater branch growth. In addition these large branches were found in the northern aspect of the crowns. So while large branches may carry a greater respiratory cost (Long and Smith 1990), the higher levels of solar radiation available from this aspect

meant that the increased leaf area was displayed effectively.

Individual branch leaf area increased strongly with branch size but the rate of increase declined with crown depth regardless of thinning (Table 6.2). Similar patterns of leaf area display have been found in other studies of *E. nitens* (Battaglia et al. 1998; White et al. 1998). Similar changes in this relationship were found in *P. taeda* but differences with crown depth narrowed after fertilizer treatment, suggesting that this decline was due to limitations by nitrogen as well as limitations by light (Gillespie et al. 1994). *L* of mature canopies of *E. nitens* generally increases following application of N fertilizer (P. Smethurst, pers. comm.[2]). Further research is required to determine if this is due to an increase in branch size or to a change in the relationship between branch size and branch leaf area with crown depth.

Thinning resulted in larger branches in the lower section of the crown. If thinning is carried out before the live crown has lifted beyond a specified height, large branches can degrade wood quality if a pruning regime is not implemented. Silvicultural regimes developed for *E. nitens* sawlog plantations incorporate a pruning system which ensures the production of knot-free wood in the first 6 m of the stem from its base (Forestry Tasmania 1999).

6.4.2 Vertical distribution of leaf area

The vertical distribution of leaf area of the unthinned *E. nitens* trees was skewed towards the top of each crown, but there was a shift towards a 'normal' distribution with increasing dominance. In a closed canopy, differences in light availability are inevitably associated with tree height and more suppressed trees show an upward

[2] Dr. Philip Smethurst, CSIRO/CRC-SPF, GPO Box 252-12, Hobart 7001, Tasmania, Australia

shift in vertical leaf area distribution compared with more dominant trees (Maguire and Bennett 1996; Xu and Harrington 1998). After *Eucalyptus* stands reach the point of canopy closure, leaf area index often declines (Beadle et al. 1995). This decline is generally attributed to a loss of leaf area from the base of the tree crowns due to low light levels (Mäkelä and Vanninen 1998). This loss of leaf area might be expected to cause a re-distribution of leaf area towards the top of the canopy. High intensity thinning of a stand either before or after canopy closure sustains or improves the light environment of the lower crown and a less-skewed leaf area distribution in the crowns of thinned trees might be expected. In this study, the improved light conditions after thinning resulted in the retention and continued growth of live branches at the base of the crown. This shifted the vertical distribution of leaf area towards a 'normal' distribution and the influence of relative dominance was muted due to the openness of the canopy. These distributions were similar to those of thinned and unthinned *P. contorta* where the foliage of unthinned trees was displaced towards the crown top (Gary 1978). As leaf area distribution in thinned trees was not related to dominance, the more 'normal' distribution of leaf area possibly reflects the optimal leaf area distribution for an individual *E. nitens* tree. A leaf area distribution with a downward shift of the layer with maximum leaf area towards crown base may be more optimal by maximising light harvesting and minimising self shading (Kellomäki and Wang 1997).

As with other tree species (Vose 1988; Mori and Hagihara 1991), the Weibull function provided a realistic description of vertical leaf area distribution of mid-rotation *E. nitens* trees. Thinning shifted the shape of this distribution towards 'normal' and, due to the lack of correlation with tree size, an average value of α

and β parameters could be used to describe vertical leaf area distribution in canopy models. The vertical profile of unthinned trees in closed-canopy stands was not normally distributed and appears to be related to relative dominance. The use of average parameters for unthinned crowns is not therefore recommended. However the use of the Weibull model may be valid in describing the vertical leaf area distribution of the entire canopy.

Differences in horizontal distribution of leaf area were not examined as part of this study but may exist between thinning treatments. However, stand density and *L* had no influence on horizontal distribution of foliage in *P. taeda*, suggesting that within-crown light distribution determines this structural feature rather than the light environment of the canopy as a whole (Xu and Harrington 1998).

6.4.3 Leaf area index development

The observed *L* values for the fully closed, unthinned canopy at each of the three sites were in the range of those reported for *Eucalyptus* stands (Linder 1985; Beadle 1997). The initial increases in *L* following thinning (Table 6.4) were generally independent of residual stocking but in the longer-term, the rate of change in *L* was higher in the more heavily thinned treatments (Figure 6.7a). While absolute changes in *L* were similar across all thinning treatments, the relative rate of increase was much greater for the stands of lower stocking. This may be due to a higher proportion of assimilated carbon being allocated to canopy development in these widely spaced stands (Bernardo et al. 1998). Leaf area density was not changed by thinning due to similar branch angle, branch cross-sectional area - length, and branch cross-sectional area - leaf area relationships. As thinning did not alter leaf area density and as the change in crown width will eventually be structurally limited, the maximum leaf area of a tree may be

determined by the maximum crown length a site can support. Therefore, if maximum crown length and width at a site are known, a maximum leaf area per tree can be estimated and the minimum residual stocking which can regain the site's maximum L can also be estimated.

For thinned stands, the change in leaf area per tree was strongly related to the change in mean crown length (Figure 6.8). Change in tree leaf area is a function of both change in crown width and change in crown length. However the change in crown length appears to be the stronger driving variable in these stands as the change in crown width will ultimately be limited by structural support requirements. The unthinned treatment showed less of a relationship between change in mean leaf area per tree and change in mean crown length. The change in mean crown length may be overestimated for this treatment as of the 100 trees ha^{-1} sub-sample measured for total height and crown length, 50 trees ha^{-1} were the dominant trees in the treatment. So the true mean change in crown length for the unthinned stand may be much lower.

6.5 Conclusions

Results from this study have described the effect of thinning on branch size and distribution, crown shape and canopy development. A move towards uniform vertical leaf area distribution with increase in inter-tree spacing was observed. This implies that simple assumptions about the interception and attenuation of light can be made on an individual tree basis for heavily thinned or widely spaced stands. However, despite relatively large increases in L after thinning, heavily thinned stands are unlikely to return to full canopy closure. The crown structure and leaf area relationships described in this paper can be used to calculate the light

interception of trees in stands which have been heavily thinned. The Beer-Lambert law for estimation of light attenuation is more appropriate for closed canopies. Thus, tree growth models that consider light interception as a function of crown size and shape will be most suited to accurately reflect the conditions of a thinned stand and provide good predictions of growth (eg. Courbaud 2000).

Longer-term changes in the amount and display of leaf area imply changes to the level of water use after thinning. In the following chapter, the relationship between thinning intensity and tree water use is investigated using a recently thinned plantation.

Chapter 7. Tree sap flow and stand transpiration following thinning

7.1 Introduction

Water use by trees is driven by a number of environmental variables. These include vapour pressure deficit (Oren et al. 1999), net radiation (Zotz et al. 1998), windspeed and temperature. Water use is also influenced by the availability of soil water within the rooting zone of trees (Teskey and Sheriff 1996; David et al. 1997). The impact of these variables on the amount of water transpired depends on tree leaf area (Vertessy et al. 1995) and the stomatal behaviour of the species (Hogg and Hurdle 1997; White et al. 1999a).

Thinning of *E. nitens* plantations under the proposed regime (Forestry Tasmania 1999) converts the stands from closed to open canopies. Thus, after thinning, individual trees have greater access to site resources. In the absence of water stress, exposure of crowns to greater levels of incident light should increase individual tree growth. However the increase in growth rate of *Quercus petraea* (Matt.) Liebl. trees following thinning was attributed to an alleviation of tree water stress through fewer trees extracting soil water (Bréda et al. 1995). Levels of available water may be further enhanced after thinning by an increase in the amount of precipitation reaching the soil surface as throughfall (Aussenac and Granier 1988). Greater crown exposure leads to changes in vapour pressure deficit and boundary layer conductance. Vapour pressure deficit was shown to be the main environmental factor affecting transpiration of an isolated walnut tree (Green 1993). A greater boundary layer conductance per tree with increase in tree spacing in *P. sitchensis* was caused by an increase in ventilation, ie. wind speed

(Teklehaimanot et al. 1991). The result is higher individual tree transpiration rates as found in *Chamaecyparis obtusa* Endl. after thinning (Morikawa et al. 1986). Conversely, lower sap velocities in smaller trees within a stand can be attributed to limited light availability (Hunt and Beadle 1998). As high-intensity thinning can alter a wide range of factors that influence growth, isolating the most important factor is difficult.

The heat pulse technique has been used to measure sap flow in a wide range of studies of the *Eucalyptus* genus (Dunn and Connor 1993; Hatton et al. 1998; Hunt and Beadle 1998; Benyon et al. 1999; O'Grady et al. 1999). The accuracy of the technique has been demonstrated by cut-tree experiments (Olbrich 1991; Vertessy et al. 1997). In addition, techniques for minimising error in scaling point sap velocity measurements to whole-tree sap flow have been developed (Hatton et al. 1990; Zang et al. 1996). This chapter describes the use of the heat pulse technique to examine the patterns of tree water use under ambient conditions in a recently thinned *E. nitens* plantation. While water use of eucalypts is generally proportional to tree or crown size (Vertessy et al. 1995; Hunt and Beadle 1998; O'Grady et al. 1999), it has been suggested that this relationship may not apply in thinned stands where the trees are experiencing a rapid change in environment (Teskey and Sheriff 1996). The study tested the hypothesis that, following thinning, water use by trees remaining in the thinned stand was proportionally higher than trees in an unthinned stand.

7.2 Materials and methods

7.2.1 Sap flow nomenclature

The sap flow nomenclature system recommended by Edwards et al. (1996) was

adopted for this study. 'Sap velocity' was used to describe the speed of water movement through the tree and was calculated using the known volume fraction of wood and water in the sapwood, and corrected for wounding. Heat pulse velocity (v_h), heat pulse velocity corrected for wounding (v'_h), and sap velocity (v_s) were expressed in units of mm s^{-1}. 'Sap flow' was used to describe the volume of water movement through the stem and was calculated as the product of sap velocity and sapwood area. Sap flow (Q) was expressed in units of m^3 day^{-1}.

7.2.2 Sap flow measurements

Sap flow was measured in the Creekton thinning trial (see Chapter 2 for site and experimental details) using eight sapflow sensors (Greenspan Technology Pty. Ltd., Warwick, Queensland, Australia). Measurements commenced four months after thinning and were carried out over a three-month period during the 1997-98 growing season. The trees in each thinning treatment were grouped into four classes based on diameter at breast height (DBH). Two reference trees were used in combination with a set of roaming sensors, deployed across thinning treatments and size classes for periods ranging from three to fourteen days. One reference tree was randomly selected from the highest frequency DBH class in an unthinned plot. The other reference tree was randomly selected from the highest frequency DBH class in a nearby 250 trees ha^{-1} thinned plot. The two reference trees were each measured continuously using two loggers and four probesets, one in each of the northern, southern, eastern and western axes. Measurements began on 8 December 1997 and finished on the 2 March 1998. Probes were re-installed in the reference trees after 28-day periods.

Roaming sensors (one logger, two probesets per tree) were used on 47 trees across all four thinning treatments. Probeset 1 was inserted in the northerly aspect of

each tree with thermistor pairs placed at depths of 15 and 10 mm inside the cambium. Probeset 2 was inserted in the easterly aspect of the tree so that the thermistor pairs were placed at depths of 10 and 5 mm inside the cambium. The probesets were at 1.3 m tree height and positioned so that no branch or bark deformity occurred within 0.15 m above or below the point of insertion. The heat pulse units were wrapped in reflective aluminium foil to act as a solar radiation shield. Each measurement used a 1.6 s heat pulse at 15 min intervals. v_h values greater than 150 s were considered to represent zero sap flow. The stem diameter at 1.3 m and total height of each of the sample trees were measured upon completion of the experiment. v_h values were corrected for wounding effects (v'_h) assuming a wound diameter of 2.2 mm (Swanson and Whitfield 1981). v_s was calculated as (Barrett et al. 1995):

$$v_s = \frac{v'_h \rho_b (C_w + mC_s)}{\rho_s C_s} \qquad 7.1$$

where C_w was the specific heat capacity of wood (1.38 x 10^6 J g^{-1} $°C^{-1}$), C_s was the specific heat capacity of sap (water) (4.19 x 10^6 J g^{-1} $°C^{-1}$), ρ_b was the basic density of dry sapwood (kg m^{-3}), ρ_s was the basic density of sap (1 x 10^3 kg m^{-3}) and m was the moisture content of sapwood (kg water kg^{-1} wood dry weight).

7.2.2.a Sapwood area and volume fractions

Four wood samples (one from each of northern, eastern, southern and western aspects) were taken at the completion of sampling of each tree to estimate sapwood area at the height of sapflow measurement. A 5 mm increment corer extracted the samples. Sapwood width was estimated by holding the diameter cores over a light-table so that the sapwood vessels involved in water transport

could be clearly seen as points of light (R. Benyon pers. comm.[3]). Mean sapwood width was combined with bark width and diameter over bark measurements to estimate sapwood area by subtraction.

Two additional cores (one each from northern and eastern aspects) were taken to gravimetrically determine the volume fractions of wood and water in the sapwood of each tree.

7.2.2.b Radial variation

Sapflow variation in the radial axis of the tree was accounted for by measuring a sapflow profile in each of the roaming sample trees at the completion of the measurement period (after Zang et al. 1996). On warm, clear days probesets were inserted in the southern and western aspects of the tree. Radial profiles were constructed for each of these two axes by moving the sensors in 5 mm increments two minutes before the heat pulse was fired (10 min interval between pulses). The southern probeset was pushed into the tree while the western probeset was pulled out of the tree. These profiles were used with corresponding point measurements from the northern and eastern axes to determine a correction co-efficient for the routine point measurements (an average of point to moving ratios, weighted by sapwood depth). The correction co-efficient for northern and eastern stationary sensors was applied to the northern and eastern v_s values made at 10 mm under the cambium.

7.2.3 Weather data

Measurements of air temperature (T), relative humidity (h), vapour pressure deficit (D), wind speed (u) and rainfall (r) were made at a weather station

[3] Dr. Richard Benyon, CSIRO Forestry and Forest Products, Mt. Gambier, SA 5290, Australia

established 500 m from the experimental site. A screened Vaisala probe measured T, h and D. u was measured with a cup anemometer at a height of 6 m. Rainfall was measured by a tipping-bucket rain gauge with a 0.2 mm bucket. A 21X data logger (Campbell Scientific, Shepshed, UK) was programmed to sense T, h, D, u and r every five minutes. Hourly averages of T, h, and D and hourly totals of u and r were recorded. Technical problems were encountered at the weather station with the measurements of total solar radiation (Q) and net radiation (R_n) during the sap flow measurement period. Consequently, Q and R_n data from a weather station located at Lewisham (72 km from the experimental site) was used. At Lewisham, Q and R_n were measured with a Li-Cor LI-200s pyranometer (Li-Cor Inc. Lincoln, NB, USA) and a Fritschen type net radiometer respectively. A 21X data logger (Campbell Scientific, Shepshed, UK) was programmed to sense Q and R_n every five minutes. Hourly totals were recorded.

7.2.4 Plot transpiration

Tree sapflow measurements were integrated upwards for daily stand-level transpiration (E_m);

$$E_m = L_j^* \left(\frac{\sum_{i=1}^{n} \frac{Q_{ij}}{L_{ij}}}{n} \right) \qquad 7.2$$

where L_j was leaf area index of the jth thinning treatment, Q_i was daily sap flow of the ith tree in the jth thinning treatment and L_i was leaf area of the ith tree in the jth thinning treatment. L from Li-Cor LAI-2000 (PCA) measurements during March 1998 were applied.

Predicted daily transpiration rates (E_p) were calculated using the Penman-

Monteith equation (Monteith 1965) as a sub-model of PROMOD (Battaglia and Sands 1997), a process-based productivity model. Aerodynamic conductance, g_a, was estimated from the maximum boundary layer conductance observed in an irrigated *E. globulus* and *E. nitens* plantation (White et al. 1999a). Estimates of canopy conductance, g_c, were made using a phenomenological model developed for *E. globulus* and *E. nitens* to consider the effect of D, T, Q and water stress on maximum stomatal conductance (White et al. 1999a). Canopy transpiration was calculated from g_c by using a dimensionless coupling coefficient (Ω) (Jarvis and McNaughton 1986; White et al. 1999b):

$$\Omega = \frac{\beta + 1}{\beta + 1 + g_a / g_c} \qquad 7.3$$

where:

$$\beta = \frac{\Delta \lambda}{c_p P} \qquad 7.4$$

where Δ was the rate of change of saturated water vapour pressure with temperature, λ was the latent heat of vaporisation, c_p was the specific heat of air and P was atmospheric pressure.

An imposed rate of transpiration (E_{imp}), assuming that air vapour pressure deficit (D) was imposed at the canopy surface ($\Omega = 0$) was calculated as:

$$E_{imp} = \frac{\left(c_p / \gamma\right) g_c D}{\lambda} \qquad 7.5$$

where γ was the psychrometric constant.

An equilibrium transpiration rate ($\Omega = 1$) was calculated as:

$$E_{eq} = \frac{\beta R_n}{(\beta+1)\lambda} \quad 7.6$$

E_{imp} and E_{eq} were used to calculate E_p:

$$E_p = \Omega E_{eq} + (1-\Omega)E_{imp} \quad 7.7$$

Daily measurements of maximum and minimum T, Q and r were combined with L to run PROMOD. The effect of thinning was incorporated into the model by a simple canopy fraction factor (C_f). The C_f value was an estimate of the projected canopy area as a fraction of ground area using a mean crown radius value of 2.0 m (Medhurst, unpublished data). In the model, C_f was used to scale up the L of the thinned stand to that of a closed canopy (L_c):

$$L_c^* = \frac{L^*}{C_f} \quad 7.8$$

L_c was used in the model to make closed canopy predictions of daily transpiration (E_p'). E_p' values were scaled back to the E_p for each thinned stand using C_f:

$$E_p = E_p^{'}.C_f \quad 7.9$$

7.2.5 Data analysis

Mean daily sap velocity was calculated across a 24 h period. Sap flow was calculated as sap velocity multiplied by sapwood area. Mean daily sap velocity and sap flow for the roaming sample trees were regressed against values from the reference trees to estimate water use of sample trees for the entire measurement period. The reference tree that produced the stronger relationship was used. While seasonal fluctuations in leaf area index of eucalypt species do occur (Pook 1984), leaf area was assumed to have remained constant during the 84-day period. An

allometric relationship between stem sapwood area and leaf area for *E. nitens* (equation 5.12) was used to estimate leaf area of all measured trees. The leaf area of each tree was used to estimate mean sap flow per unit leaf area (Q_l) across the 84-day measurement period.

Analysis of variance was used to analyse the effect of thinning on volume fractions of wood (V_w) and water (V_h), mean daily sap velocity, sap velocity correction coefficients, and sap flow per unit leaf area. The GLM module in SAS (SAS Institute Incorporated 1990) was used for the analysis. The least squares method was used to determine means and standard errors.

The effect of thinning treatment on the relationship between stem basal area and mean daily sap flow was investigated using regression analysis. A two-sided natural logarithmic transformation was carried out to provide homoscedacity of variance. A group regression procedure was used to test if the deviance of the model is significantly increased by generalising the slope and intercept across thinning treatments (McPherson 1990 p. 549).

Measured and predicted daily plot transpiration values for each thinning treatment were compared using paired *t*-tests.

7.3 Results

7.3.1 Tree characteristics

A similar range of tree sizes was sampled in each of the thinning treatments (Table 7.1). Tree leaf area (one-sided or projected) ranged from 10.0 to 99.6 m² for trees in the unthinned treatment and from 11.7 to 115.2 m² for trees in the thinned treatments.

Table 7.1 Summary statistics of diameter at breast height for sampled trees in each thinning treatment.

Treatment	n	Mean DBH (mm)	Mean SE	Min. DBH (mm)	Max. DBH (mm)
100 trees ha^{-1}	11	212	12.8	133	271
250 trees ha^{-1}	13	197	14.0	127	279
600 trees ha^{-1}	11	190	12.4	131	255
unthinned	12	187	13.9	118	283

Sapwood area at breast height ranged from 0.0049 to 0.021 m^2 in trees from the unthinned treatment and from 0.0045 to 0.023 m^2 in trees from the thinned treatments (Table 7.2). Sapwood area was strongly related to stem cross-sectional basal area (Figure 7.1). This relationship was not affected by thinning ($p > 0.05$). The volume fractions of wood (V_w) and water (V_h) in the sapwood of trees in the unthinned treatment ranged from 0.24 to 0.31 and 0.57 to 0.69 respectively. V_w and V_h in the sapwood of trees in the thinned treatments ranged from 0.24 to 0.31 and 0.60 to 0.69 respectively (Table 7.2). No significant difference in V_w and V_h was found with thinning treatment ($p > 0.05$).

Table 7.2 Summary statistics of tree size and sapwood parameters for the 47 sapflow sample trees at Creekton. Values in parentheses show mean standard errors.

Thinning treatment	Mean sapwood area ($mm^2 \times 10^{-2}$)	Mean sapwood width (mm)	Mean volume fraction of water V_h	Mean volume fraction of wood V_w
100 trees ha^{-1}	139.1 (15.4)	25 (2)	0.63 (0.01)	0.28 (0.01)
250 trees ha^{-1}	116.9 (14.1)	23 (1)	0.64 (0.01)	0.29 (0.01)
600 trees ha^{-1}	104.4 (12.0)	21 (1)	0.65 (0.01)	0.28 (0.01)
unthinned	105.1 (13.8)	21 (1)	0.63 (0.01)	0.29 (0.01)

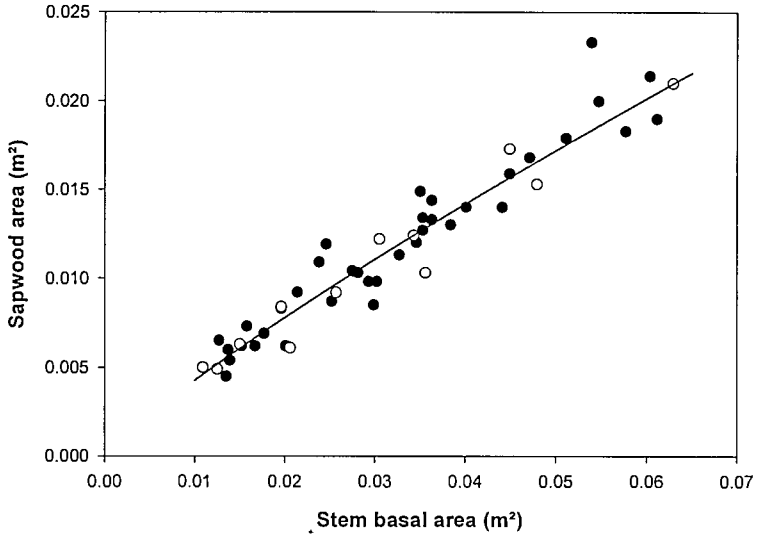


Figure 7.1 Relationship between sapwood area and stem basal area (over bark) for trees in the thinned and unthinned treatments at Creekton. Pooled regression relationship; $y = 0.23x^{0.866}$, $r^2 = 0.93$. (●=thinned treatment, ○=unthinned treatment)

7.3.2 Radial variation in sap velocity

Maximum v_s with depth usually occurred between 10 and 15 mm (eg. Figure 7.2). A comparison of northern and eastern values generally showed higher v_s at the northern aspect but this was not always the case. The radial variation in v_s for similarly-sized trees varied between thinning treatments (Figure 7.2). The correction coefficients calculated for the northern aspect at a depth of 10 mm ranged from 0.20 to 2.26 for trees in the thinned treatments and from 0.52 to 1.79 for trees in the unthinned treatment. There was no significant difference between the correction coefficients calculated for the northern and eastern aspects ($p >$ 0.05, paired t-test). Mean correction coefficient values increased with increasing thinning intensity (Table 7.3). The northern and eastern correction coefficients of trees in the 100 and 250 trees ha^{-1} treatments were significantly higher than in the

unthinned treatment ($p < 0.05$).

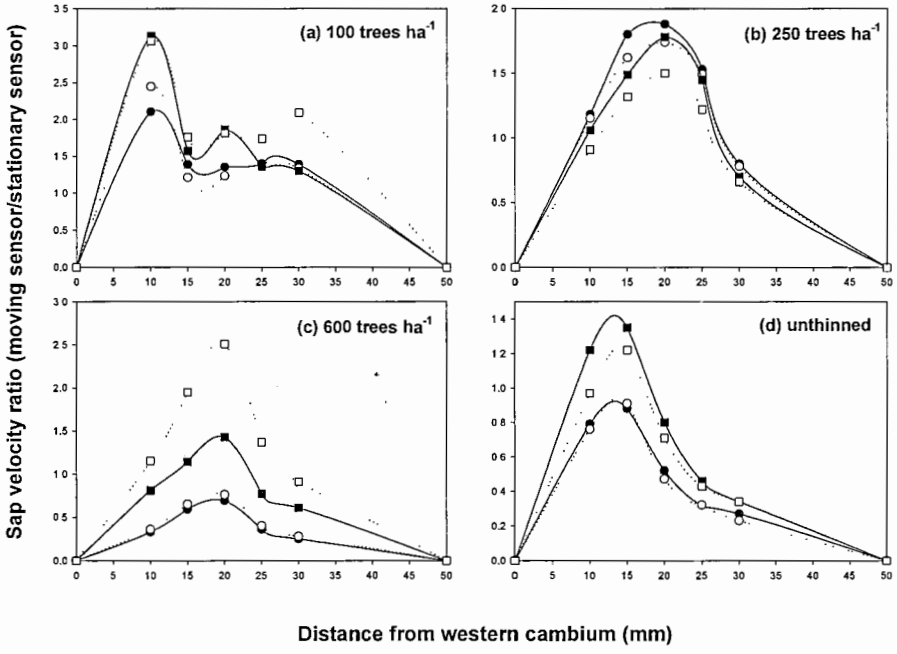


Figure 7.2 Examples of sap velocity ratio profiles for trees from the second DBH class in the (a) 100 trees ha^{-1}, (b) 250 trees ha^{-1}, (c) 600 trees ha^{-1}, and (d) unthinned treatment at Creekton. The moving sensor was located in the western axis. The ratios for the northern and eastern stationary sensors are shown. Symbols show 15 mm under northern cambium (—●—);10 mm under northern cambium (····○····);10 mm under eastern cambium (—■—) and 5 mm under eastern cambium (····❑····). Note that differing scales have been used for the y-axis.

Table 7.3 Mean and standard error of sap velocity correction coefficients by thinning treatment, Creekton.

Thinning treatment	Northern aspect		Eastern aspect	
	Mean	± 1 SE	Mean	± 1 SE
100 trees ha^{-1}	1.25	0.12	1.10	0.09
250 trees ha^{-1}	1.16	0.13	1.00	0.08
600 trees ha^{-1}	0.83	0.10	0.89	0.07
unthinned	0.77	0.12	0.71	0.06

7.3.3 Reference tree water use

The mean daily sap flow (Q) of the reference tree in the unthinned treatment (stem diameter of 168 mm at start of measurement) was 0.033 m^3 day^{-1} (range 0.009 to 0.052 m^3 day^{-1}). Mean daily Q of the reference tree in the 250 trees ha^{-1} treatment (stem diameter of 201 mm at start of measurement) was 0.060 m^3 day^{-1} (range 0.013 to 0.095 m^3 day^{-1}). Both followed a similar pattern of transpiration across the 84-day measurement period (Figure 7.3a). The difference in Q between the two trees was reduced on completely overcast days (eg. days 4, 51 and 59). Daily sap flow per unit leaf area (Q_l) was generally higher for the reference tree in the 250 trees ha^{-1} treatment (Figure 7.3b). Mean daily Q_l for the unthinned treatment reference tree was 0.0015 m^3 m^{-2} day^{-1} (range 0.0003 to 0.0023 m^3 m^{-2} day^{-1}). Mean daily Q_l for the reference tree in the 250 trees ha^{-1} treatment was 0.0018 m^3 m^{-2} day^{-1} (range 0.0004 to 0.0028 m^3 m^{-2} day^{-1}).

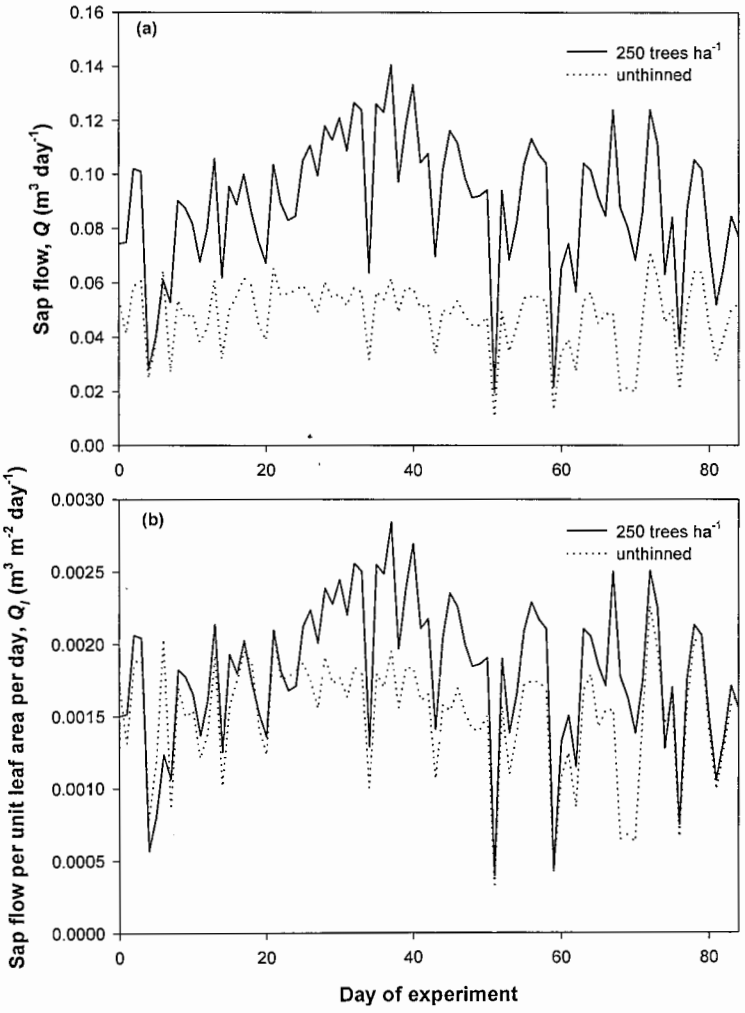


Figure 7.3 Daily (a) sap flow (m^3 day^{-1}) and (b) sap flow per unit leaf area (m^3 m^{-2} day^{-1}) for the reference trees at Creekton. Measurement commenced on 8 December 1997 and finished on 2 March 1998.

The reference trees showed differences in diurnal variation of Q_l. These differences were greatest on warm and sunny days (Figure 7.4a) and least on cooler and overcast days (Figure 7.4b).

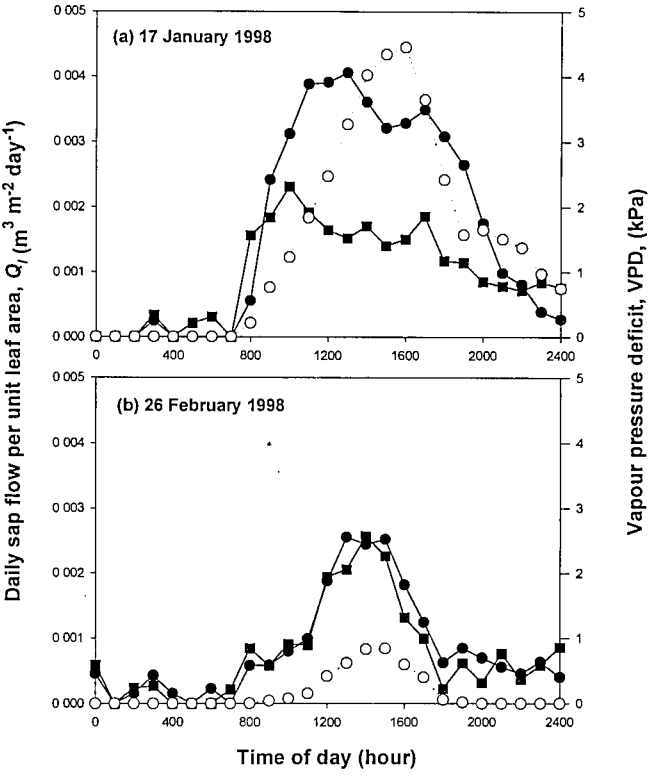


Figure 7.4 Diurnal variation in Q_l for the reference trees in the 250 trees ha^{-1} treatment (—●—) and the unthinned treatment (—■—) for (a) 17 January 1998 and (b) 26 February 1998. Variation in vapour pressure deficit (D) is also shown (····○····).

Details of the regressions of daily sap velocity of sample trees against that of the reference trees are listed in Table 7.4. Coefficients of determination (r^2) ranged from 0.47 to 0.99 but were generally high (half of trees > 0.90).

Table 7.4 Details of linear regressions of mean daily sap velocity against either the unthinned or thinned treatment reference tree. Four trees that showed zero flow are omitted from this table.

Tree ID	No. of measurement days	Reference tree	r^2	p value	Intercept	slope
100-1 A	6	unthinned	0.90	0.002	-0.0042	0.722
250-1 A	4	unthinned	0.75	0.089	0.0007	0.703
600-1 A	8	unthinned	0.94	0.000	0.0086	0.657
Con-1 A	4	unthinned	0.89	0.036	0.0049	0.696
100-2 A	8	250 trees ha^{-1}	0.81	0.004	0.0049	0.612
250-2 A	14	250 trees ha^{-1}	0.90	0.000	-0.0036	0.789
600-2 A	8	250 trees ha^{-1}	0.83	0.001	-0.0004	0.643
Con-2 A	6	250 trees ha^{-1}	0.93	0.001	-0.006	0.554
100-3 A	8	250 trees ha^{-1}	0.69	0.007	-0.0053	0.566
250-3 A	6	250 trees ha^{-1}	0.97	0.000	0.0131	0.473
600-3 A	6	250 trees ha^{-1}	0.73	0.019	-0.0163	0.595
con-3 A	9	250 trees ha^{-1}	0.79	0.000	0.0004	0.207
100-4 A	8	250 trees ha^{-1}	0.58	0.017	0.0118	0.591
250-4 A	4	250 trees ha^{-1}	0.87	0.163	0.012	0.363
100-1 B	6	250 trees ha^{-1}	0.94	0.001	0.0019	0.612
250-1 B	7	250 trees ha^{-1}	0.66	0.017	0.0191	0.550
600-1 B	7	unthinned	0.88	0.001	-0.0135	1.280
con-1 B	7	250 trees ha^{-1}	0.94	0.000	0.0002	0.568
100-2 B	5	250 trees ha^{-1}	0.98	0.001	0.0045	0.820
250-2 B	6	250 trees ha^{-1}	0.98	0.000	0.0012	0.528
600-2 B	6	unthinned	0.95	0.001	-0.0141	0.782
con-2 B	5	unthinned	0.92	0.007	-0.0212	1.170
100-3 B	5	250 trees ha^{-1}	0.98	0.001	-0.0011	0.572
250-3 B	5	250 trees ha^{-1}	0.88	0.012	-0.0009	0.495
600-3 B	7	250 trees ha^{-1}	0.85	0.002	-0.0046	0.419
250-4 B	8	250 trees ha^{-1}	0.89	0.000	-0.0080	1.050
600-4 B	7	unthinned	0.47	0.054	-0.0036	0.513
con-4 B	9	unthinned	0.95	0.000	-0.0020	0.296
100-1 C	7	250 trees ha^{-1}	0.95	0.000	-0.0074	0.855
250-1 C	7	250 trees ha^{-1}	0.95	0.000	-0.0046	1.020
600-1 C	6	250 trees ha^{-1}	0.99	0.000	0.0178	0.574
con-1 C[1]	7	250 trees ha^{-1}	0.94	0.000	-0.0111	1.540
100-2 C	8	unthinned	0.80	0.002	-0.0064	0.942
250-2 C	5	250 trees ha^{-1}	0.92	0.006	0.0029	0.860
600-2 C	5	250 trees ha^{-1}	0.94	0.005	-0.0064	0.899
con-2 C	6	250 trees ha^{-1}	0.69	0.051	0.0016	0.237
100-3 C	6	unthinned	0.77	0.013	0.0009	1.350
250-3 C	6	250 trees ha^{-1}	0.96	0.000	-0.0103	0.974
600-3 C	6	250 trees ha^{-1}	0.97	0.000	-0.0070	0.512
con-3 C	5	unthinned	0.88	0.011	-0.0051	0.390
100-2 D	6	250 trees ha^{-1}	0.99	0.000	0.0339	0.780
250-4 C	7	250 trees ha^{-1}	0.88	0.001	-0.0135	1.090
600-4 C	6	unthinned	0.92	0.002	0.0008	0.809

[1]outlier (see section 7.4)

7.3.4 Sap velocity

A sample tree in the unthinned treatment that produced very high sap velocity values was considered an outlier and was omitted from further analysis. The tree was unrepresentative of the treatment, as it was located in a natural drainage line at the base of a slope. Within each treatment, mean sap velocity across the measurement period was independent of tree cross-sectional area ($p > 0.05$). The mean sap velocities of trees in the 100 and 250 trees ha^{-1} treatments (0.042 and 0.041 mm s^{-1} respectively) were significantly higher than that of trees in the unthinned treatment (0.019 mm s^{-1}) ($p < 0.05$). The mean sap velocity of trees in the 600 trees ha^{-1} treatment (0.030 mm s^{-1}) was not significantly different to that of the unthinned treatment.

7.3.5 Whole-tree water use

Mean daily sap flow was correlated with stem basal area at breast height (Figure 7.5, $p<0.01$). The effect of thinning treatment was significant for the slope of the log-log relationship ($p < 0.05$). The slope decreased with increasing thinning intensity, indicating that the sap flow in the smaller trees increased as a result of thinning, while sap flow in the larger trees remained largely unchanged by thinning treatment.

The daily sap flows per unit leaf area (Q_l) from each treatment were compared. Trees in the 100 and 250 trees ha^{-1} treatments had a significantly greater Q_l than trees in the unthinned treatment ($p < 0.05$). Trees in the 600 trees ha^{-1} treatment had similar Q_l to trees in the unthinned treatment (Figure 7.6).

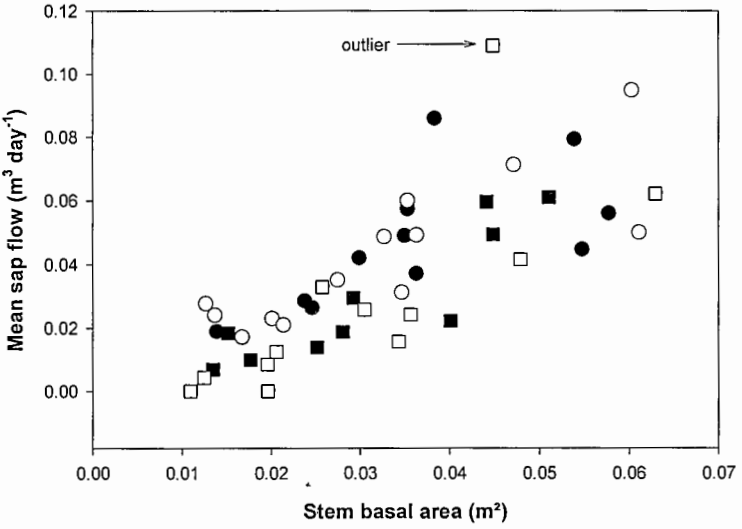


Figure 7.5 Relationship between mean daily sap flow and stem basal area (over bark) by thinning treatment. (●=100 trees ha^{-1}, ○=250 trees ha^{-1}, ■=600 trees ha^{-1}, and □=unthinned). The outlier, tree con-1C (see Table 7.4), was not used in the regression analysis (see Section 7.3.5).

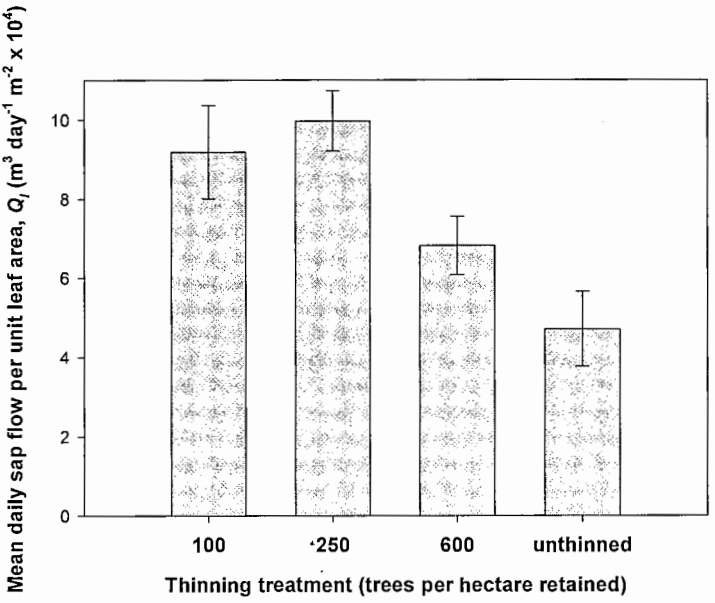


Figure 7.6 Mean daily tree sap flow per unit leaf area (Q_l) by thinning treatment (retained trees per hectare), Creekton thinning trial. Error bars show mean standard errors.

7.3.6 Plot transpiration

Mean daily plot transpiration (E_m) of the unthinned stand at Creekton was 2.6 mm day^{-1}. The maximum and minimum measured rates were 4.0 and 0.6 mm day^{-1} respectively. Mean E_m of the 100, 250 and 600 trees ha^{-1} thinning treatments were 0.6, 1.0, and 1.4 mm day^{-1} respectively. This represented 23, 36 and 55 per cent respectively, of the mean transpiration rate of the unthinned stand.

Plotting daily stand transpiration against mean daily D showed transpiration reached a plateau above D values of 0.5 kPa for all thinning treatments (Figure 7.7).

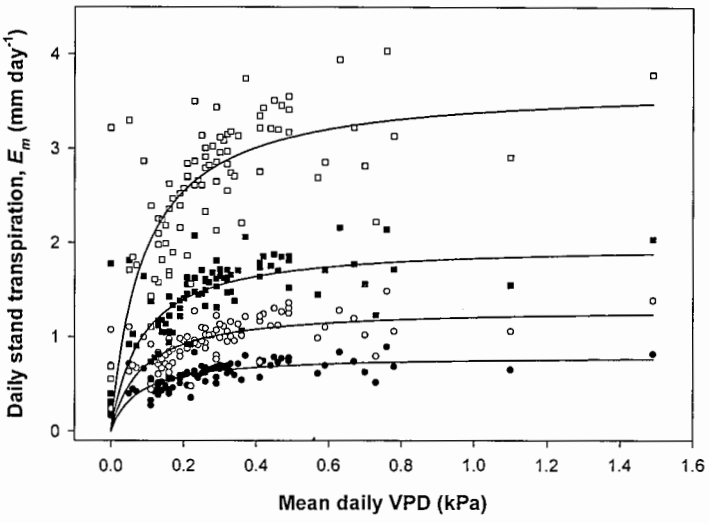


Figure 7.7 Measured daily stand transpiration as a function of mean daily vapour pressure deficit. (● = 100 trees ha^{-1}, ○ = 250 trees ha^{-1}, ■ = 600 trees ha^{-1}, □ = unthinned control)

In general, predicted daily plot transpiration (E_p) was in agreement with measured values (Figure 7.8a—d). However, the predicted values were considerably higher than measured values on days of high maximum temperature and high mean D (see Figure 7.9b,c; day nos. 37, 40, 45 and 56). Mean E_p was 0.8, 1.3, 2.1 and 2.8 mm for the 100, 250, 600 trees ha^{-1} and unthinned treatments respectively.

Total rainfall during the 84-day measurement period was 230 mm. Total E_m (218 mm) and E_p (235 mm) from the unthinned stand during this period were similar to total rainfall. Total E_m for the 100, 250 and 600 trees ha^{-1} treatments during this period were, respectively, 50, 84 and 118 mm. Total E_p for the 100, 250 and 600 trees ha^{-1} treatments during this period were, respectively, 67, 109 and 177 mm.

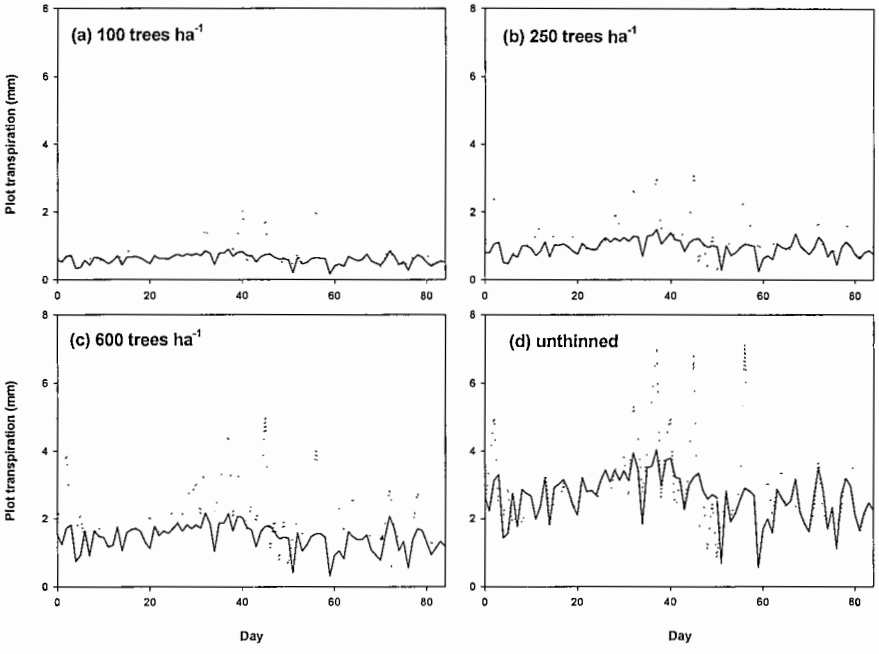


Figure 7.8 Measured (———) and predicted (·····) daily plot transpiration for the (a) 100 trees ha^{-1}, (b) 250 trees ha^{-1}, (c) 600 trees ha^{-1}, and (d) unthinned treatments at Creekton from 8 December 1997 to 2 March 1998. Measured transpiration rates are from sapflow sensors. Predicted transpiration rates are from equations 7.3 to 7.9.

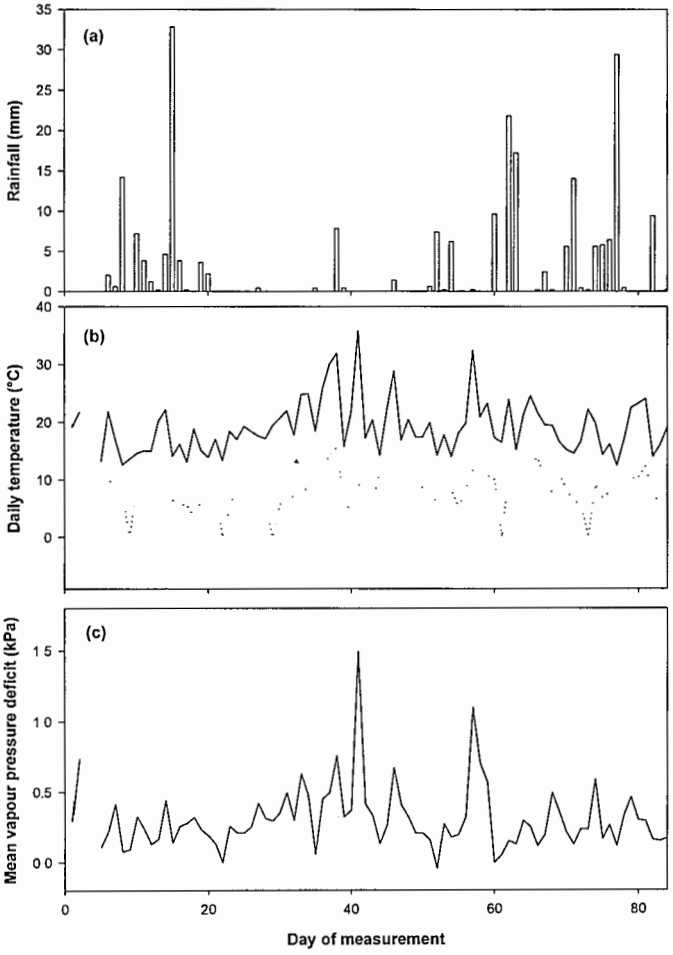


Figure 7.9 Daily observations of (a) total rainfall, (b) maximum (———) and minimum (·····) temperature, and (c) mean vapour pressure deficit from the Creekton meteorological station.

7.4 Discussion

7.4.1 Radial variation in sapflow

Changes in the relationship between tree size and daily water use were found four months after thinning. These changes were driven largely by differences in the radial variation of sap velocity with thinning treatment. For *Eucalyptus* stands not undergoing rapid change in leaf area index, strong and consistent relationships between tree size and water use have been reported (Calder et al. 1992; Hatton et al. 1995; Vertessy et al. 1997; Hunt and Beadle 1998; O'Grady et al. 1999). The suggestion of Teskey and Sheriff (1996) that proportional water use by large and small trees, in terms of leaf area, may not apply to recently thinned stands was supported by the findings of this study. Any major alteration in crown structure or root patterns and volume between the thinning operation and the measurement period is unlikely, due to the slow growth response to thinning observed in this trial (see Chapter 3). This suggests that the changes in transpiration after thinning were determined primarily by changes in climatic demand (Green 1993) and/or physiological responses to an increase in soil water availability (Calder 1992).

Large radial variation in sap velocity was found in this study. Radial variation in sap velocity has been found previously in *E. nitens* (Hunt and Beadle 1998) and in other *Eucalyptus* species (eg. Dunn and Connor 1993; Hatton et al. 1995; Zang et al. 1996). Failing to account for this variability could lead to large errors in estimates of tree and stand water use (Wullschleger and King 2000). Integrating point measurements of sap velocity (v_s) to sap flow estimates (Q) for each tree was a major source of potential error in this study. Based on the correction coefficient method of Zang et al. (1996), the maximum mean potential error in Q

of individual trees with stratified sampling was 29 per cent (Table 7.3). This was in close agreement with that found by Hatton et al. (1995) (25 per cent) for a *Eucalyptus populnea* Muell. woodland. It is worth noting that the mean correction coefficient of the unthinned stand in this study (0.77) was almost identical to that measured by Zang et al. (1996) in a *E. globulus* plantation (0.78).

While between-tree variation was large, sampling intensity and stratification was sufficient to show that thinning a closed-canopy stand altered radial profiles of sap velocity. Without considering radial variation in sap velocity, the sap flow of trees after thinning was underestimated while the sap flow of trees in unthinned stands was overestimated. A more complete understanding of the change in radial variation is required before using heat pulse technology to compare tree water use under different management strategies. The technique of weighting heat pulse velocity measurements by the area of sapwood sampled (eg. Hatton et al. 1990) may not be suitable in studies where different management scenarios are being compared.

The causes behind radial variation in v_s are not well understood (Wullschleger and King 2000) although a range of hypotheses have been proposed. Studies have shown a decrease in sapwood water content with depth but this alone does not account for the change in v_s with depth (Phillips et al. 1996; Wullschleger and King 2000). Dye at al. (1991) suggested that the inner sapwood is the primary conduit for water supply to the older, lower branches of a tree. They postulated that increased shading or branch death means that the sap velocity of the inner sapwood declines because of lower transpirational demand. A high correction coefficient value using the method of Zang et al. (1996) implies that a high proportion of sapwood area is contributing to water transport. In this study, mean

correction coefficient values increased with increasing thinning intensity within the first eight months of applying the treatment. The improvement in light conditions after thinning results in increases in the level of photosynthetic activity of the lower section of the crown (see Chapter 8, Wang et al. 1995; Peterson et al. 1997). This is likely to have increased the transpirational demand from this section of the crown. If the inner sapwood is the primary conduit for supplying water to the lower section of the crown, the increase in correction coefficients with thinning lends support to the theory of Dye et al. (1991).

Axial variation in sap velocity was negligible in this study. Differences in sap velocity by aspect have generally been shown for trees with asymmetrical crowns (Vertessy et al. 1997; Hunt and Beadle 1998). As this study was carried out in a recently thinned plantation, it would be reasonable to expect symmetrical crowns across all thinning treatments. However in the longer term, asymmetrical crowns may develop after thinning (see Chapter 6) and differences in sap velocity with respect to aspect may develop.

In the short term, thinning did not alter sapwood characteristics. The volumetric fractions of water and wood in the sapwood of the sampled trees were similar across thinning treatment. These fractions have also been shown as constant with age in *E. regnans* (Dunn and Connor 1993). Higher correction coefficients with thinning may be indirect evidence of an increase in the hydraulic conductivity of sapwood (k) soon after thinning. Despite increases in soil water potential and transpiration from tree crowns soon after thinning, studies have shown that leaf water potential has remained generally unaffected (Cregg et al. 1990; Ginn et al. 1991). For this to occur, k must be increased by thinning (Jarvis 1976; Whitehead et al. 1984b). An increase in k with soil water availability was inferred from long-

term studies in *E. nitens* (White et al. 1998) and higher radial variation in sap flow in *E. nitens* was found in trees under strong inter-specific competition (Hunt and Beadle 1998). A decline in the hydraulic conductivity of sapwood (k) with distance from the cambium was found for two *Populus* species, however axial direction affected k with the side of the trees receiving greater sunlight having significantly greater k (Edwards and Booker 1984). Shelburne and Hedden (1996) found radial variation in k for *P. taeda* which could not be explained by anatomical differences in tracheids. They attributed the greater proportion of viable sapwood in trees with reduced competition to the ability to obtain the level of nutrients and water required for maintaining an effective sapwood area. In addition, the ability of trees to reverse xylem embolisms and thus restore k has been shown (Hacke and Sauter 1996; Borghetti et al. 1998). In the current study changes in the radial variation of v_s, and hence permeability, of the sapwood were evident soon after thinning. Such a change may be a feedback mechanism to avoid the development of deleterious leaf water potentials after thinning (Jarvis 1976).

7.4.2 Transpiration rates after thinning

Differences in the daily sap flow per unit leaf area (Q_l) of the two reference trees in the 250 trees ha^{-1} and unthinned treatments were greatest on the days of high sap flows. These days were characterised by high vapour pressure deficit (D). Technical difficulties associated with solar radiation measurements at the Creekton site meant that the relationship between transpiration and solar radiation could not be investigated. However, transpiration rates of thinned and unthinned stands are closely related to solar radiation levels as well as D (Morikawa et al. 1986). Increases in Q_l with thinning are likely to be caused by an increase in the amount of intercepted radiation and changes in conductances on a tree-basis. A

linear increase in tree boundary layer conductance with increasing tree spacing was found in *P. sitchensis* (Teklehaimanot et al. 1991).

E_p for the unthinned stand was in close agreement with E_m, save for days of high maximum temperature and D. The reason for lower-than-expected E_m across all thinning treatments on these days is unknown. While within the range of transpiration rates for *Eucalyptus* stands (Vertessy et al. 1995), the mean E_m of unthinned stands in this study was lower than some reported rates of mean transpiration in *E. nitens* plantations (Honeysett et al. 1992) but similar to others (Hunt and Beadle 1998). The tendency for the model to slightly over-predict transpiration rates may have been caused by the use of solar radiation data which was not collected at the Creekton site. This study used an average crown radius value but more direct measurements of tree domain have shown promise as a scalar of sap flow measurements to stand level water use (Hatton et al. 1995). Therefore a direct measure of canopy projection area in each thinning treatment is also likely to have improved the accuracy of E_p in this study. Despite the data limitations in this study, the canopy fraction factor in the Penman-Monteith model showed promise as a simple and effective method for scaling the model to predict transpiration from thinned stands.

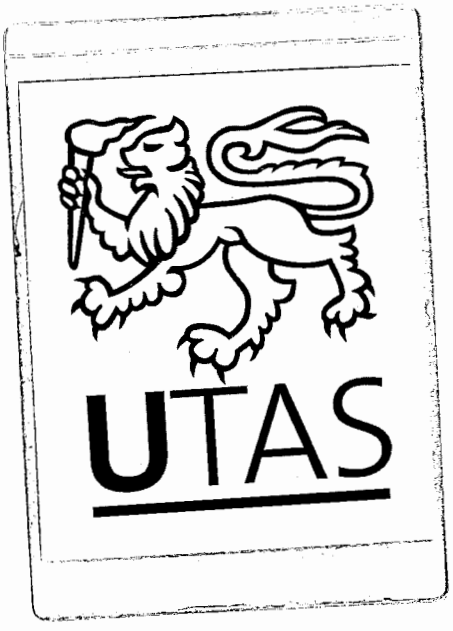
Knowledge of changes in crown structure, particularly the rate of L recovery after thinning, is important for longer-term prediction of stand water use. The higher rates of water use in retained trees following thinning would be expected to decline to the levels of trees in an unthinned stand over time as the stand approaches or regains full canopy closure. Teskey and Sheriff (1996) found that water use was proportional to leaf area five years after thinning in a *P. radiata* plantation. The rate of return to a common tree size-water use relationship across

the range of thinning treatments at Creekton will depend on the rate of canopy closure.

7.5 Conclusions

Thinning increased the water use of retained trees. Changes in the radial variation of sap flow were identified as the major cause for increased tree water use following thinning. To improve the accuracy of tree water use estimates and enable better comparisons between management options, quantifying the radial variation in sap flow when using heat pulse technology is considered essential.

In the following chapter, the changes in crown micro-environment and photosynthetic activity are examined as potential mechanisms behind the increased water use after thinning.



Chapter 8. Photosynthetic capacity and leaf nitrogen distribution

8.1 Introduction

Changes in resource levels (radiation, water, and nutrients) influence crown processes and are ultimately reflected in changes in tree growth. Understanding the effect of silvicultural treatment on resource levels and consequently on physiology and morphology of tree crowns can aid the development of models to explain the functioning of forest stands.

Light availability, foliar nitrogen levels and photosynthetic activity are all closely related. Nitrogen is an essential component of amino acids and chlorophylls required for photosynthesis. A positive association between leaf nitrogen content and photosynthetic capacity has been found for eucalypt species, including *E. globulus* (Sheriff and Nambiar 1991; Pereira et al. 1994) and *E. grandis* (Leuning et al. 1991a). On the basis of this relationship, nitrogen content can be used as a predictor of photosynthetic capacity (Leuning et al. 1991b; Leuning et al. 1995; de Pury and Farquhar 1997). A theory of nitrogen allocation predicts that the distribution of foliar nitrogen throughout the crown will maximise the total carbon gain of the crown (Field 1983). Inherent in this theory is that nitrogen will be preferentially allocated to foliage in areas of high irradiance (Givnish 1988). Studies have confirmed this relationship between nitrogen content and irradiance in tree canopies of *Prunus persica* cv. Fantasia (DeJong et al. 1989), *E. grandis* (Leuning et al. 1991a), *Juglans regia* L. (Le Roux et al. 1999) and *P. contorta* (Schoettle and Smith 1999).

Thinning of closed-canopy stands dramatically alters the light regime of the retained trees (Wang et al. 1995; Tang et al. 1999). Enhanced leaf photosynthesis after thinning has been attributed to an increase in light intensity throughout the crowns of *P. taeda* (Ginn et al. 1991; Tang et al. 1999) and *Betula papyifera* Marsh. (Wang et al. 1995). Enhanced photosynthesis as a result of thinning virtually disappears after the canopy re-closes (Gravatt et al. 1997), providing further evidence that light is crucial for driving thinning response.

The growth response to thinning has been quantified for *E. grandis* (Schönau 1984; Bonny 1991; Birk and Turner 1992), *Eucalyptus delegatensis* R.T. Bak. (Horne and Robinson 1990), *E. regnans* (Messina 1992; Gerrand et al. 1997b; McKenzie and Hawke 1999), *E. saligna* (Williamson 1979), *E. nitens* (Gerrand et al. 1997b) and *E. obliqua* (Brown 1997). However, our understanding of the mechanisms behind the growth response to thinning in eucalypts is comparatively limited. Difficulties in accessing and measuring the crowns of mature trees have been the main impediments to furthering our knowledge of physiological responses to cultural treatments (Tang et al. 1999). This chapter describes a study carried out under field conditions to examine the physiological and morphological responses of mature *E. nitens* crowns to thinning. The experiment tested the hypothesis that thinning alters the spatial pattern of photosynthetic activity in the crowns of *E. nitens* trees. Specifically, the objectives of the study were to;

(1) determine the extent to which maximum photosynthetic rates (A_{max}) of *E. nitens* are affected by thinning treatment,

(2) relate the spatial pattern of A_{max} within the crown to the changes in light environment caused by thinning, and

(3) establish if the responses of A_{max} to thinning are driven by changes in foliar nitrogen or phosphorus concentrations.

8.2 Materials and Methods

8.2.1 Treatments and experimental design

All measurements were conducted at the Creekton experimental site (see Chapter 2 for details). Three 20 m scaffolding towers were constructed to enable access to the crowns of thinned and unthinned trees. Two towers were erected in a thinned plot (250 trees ha^{-1}), each tower giving access to the crowns of two trees for gas-exchange, leaf area and leaf water potential measurements. The third tower was erected in an adjacent unthinned control plot. This tower provided access to the crowns of three trees for the same measurements. A fourth tree could also be reached for leaf area and leaf water potential measurements. The towers were constructed in September 1998 and were used for nine months.

The crown lengths of the four trees in both the unthinned and the thinned plots were used to divide the canopies into three equal vertical zones; a lower, middle and upper canopy zone. Three 1 m wide gantries were placed on the towers to give access to each of these zones. Foliage was classed as old (> 2 years of age), mature (< 2 years old but fully expanded) or apical (expanding) for each of these zones.

8.2.2 Gas-exchange measurements

Gas-exchange measurements were made on four occasions; October 1998, March 1999, April 1999 and May 1999. The first series of measurements were carried out using a CIRAS-1 Portable Photosynthesis System (PP Systems, Hitchin, Herts, UK). A Parkinson PLC-Broad leaf cuvette (area 2.5cm^2) was used to

enclose the leaves. Flow rate was 200 ml min^{-1}. The remaining series of gas-exchange measurements were made using a LCA2 open-flow gas analysis system (Analytical Development Corporation, Hoddesdon, Herts, UK). A Parkinson PLC-Broad leaf cuvette (area 6.5cm^2) was used with a flow rate of 400 ml min^{-1}. With both systems, measurements of maximum net photosynthesis (A_{max}) were made under constant light illumination using a lamp unit. A light intensity of 1500 µmol m^{-2} s^{-1} was used, with the power supplied by a 12 V 20 amp-hour car battery. A_{max} of three leaves per foliage age class in each canopy zone of each tree was measured. However, old foliage was present in the lower and middle crown zones only. Ambient CO_2 (~360 ppm) and water vapour concentrations were used. Leaf temperatures generally ranged between 15 and 25 °C, within the range of photosynthetic optimum temperature for *E. nitens* (Battaglia et al. 1996).

All measurements were carried out between 0900 and 1400 h Australian Eastern Standard Time (AEST). Two consecutive days were required to complete the sampling. The order in which the towers were measured was randomly allocated before each series of measurements.

An automatic weather station in the Creekton plantation, approximately 500 m from the experiment site, was used to measure daily maximum and minimum temperatures and relative humidity for the day before gas-exchange measurements and for the days of measurement.

8.2.3 Foliar specific leaf area and nitrogen and phosphorus concentrations

All the leaves used for measurement of gas-exchange were collected immediately following measurement to determine specific leaf area and nitrogen (N) and

phosphorus (P) concentrations. The three leaves from each foliage-class per canopy zone per tree were pooled for these measurements. Projected (one-sided) leaf area was measured using a leaf area meter (Delta-T Devices Limited, Cambridge, UK). The leaves were subsequently dried at 80 °C for 48 h, cooled and weighed, and then ground in a hammer mill and dried for a further 24 h at 80 °C. The samples were prepared for analysis by using a single acid-hydrogen peroxide technique (Lowther 1980). Analysis of total kjeldahl N and total P was carried out using a spectrophotometric flow injection analyzer (QuikChem 8000, Lachat Instruments Milwaukee, WI, USA). The N and P content of foliage was calculated using N and P concentrations and specific leaf area values.

8.2.4 Light attenuation measurements

A set of eight quantum sensors (Delta-T Devices Limited, Cambridge, UK) was used to measure the distribution of light in the crown of thinned and unthinned trees. One sensor was placed above the crown to measure incident radiation. One sensor was placed at the base of the crown at the midpoint between the tree stem and outer crown edge. Pairs of sensors were placed in the middle of the lower, middle and upper crown zones. In each zone, one sensor was placed in line with the crown edge and the second sensor was placed at the midpoint between tree stem and outer crown edge. Data were collected by a Campbell CR21X logger (Campbell Scientific, Logan, UT, USA) which was programmed to record every five minutes and store hourly totals. Measurements were taken for seven days on the northern aspect of each tree. The sensors were then moved to the southern aspect and measurements taken for another seven days.

Each sensor was calibrated against a Skye 210 PAR sensor (Skye Instruments Ltd., Wales) and the resulting calibration was used to convert mV outputs to μmol

photons m^{-2} s^{-1}.

8.2.5 Leaf area by crown zone

Diameters of the branches in each crown zone on each tree were measured at 40 mm from the branch junction. Measurements were taken at the beginning (October 1998) and at the end (June 1999) of the experiment. Crown zone positions were not altered from the October 1998 positions. Therefore the upper crown zone at June 1999 represents more than one-third of crown length because of tree height growth.

Branch leaf area was estimated using a log-log relationship between branch cross-sectional area and branch leaf area. This relationship was derived from destructive sampling of six trees at Creekton prior to thinning treatment (see Chapter 5 for details). Significant variation between crown zones (data not shown) meant a separate regression was used for each crown zone. Leaf area per zone was estimated by summing branch leaf area.

8.2.6 Leaf water potential

Leaf water potential (Ψ_l) was measured on two occasions using the four trees accessible from the scaffold towers from each of the 250 trees ha^{-1} and the unthinned treatments. All measurements were conducted using a pressure chamber (Model 650, PMS Instrument Company, Corvallis, Oregon). A series of measurements was carried out during 21 January 1999. The measurements were made on three leaves from each of the upper, middle and lower crown zones of thinned trees and on three leaves from the lower crown zone of the unthinned trees. Each set of measurements took approximately one hour. Four sets of measurements were made during the day, beginning at 0900 and ending at 1530 h

AEST.

On 3 March 1999 pre-dawn and midday leaf water potential (Ψ_{pd} and Ψ_{mid}) was measured on mature leaves excised from the lower canopy zone of the four thinned trees and the four unthinned trees. Three leaves per tree were measured. Measurements were taken between 0500-0600 and 1130-1230 h AEST.

8.2.7 Data analysis

Using data from clear days, the fraction of light (Q_f) at different positions throughout the crown was calculated as;

$$Q_f = \frac{Q_i}{Q_o} \qquad 8.1$$

where Q_i is the light intensity at the i^{th} position in the crown and Q_o is the incident light at the top of the crown. The effect of thinning on Q_f at various positions in the crown was investigated using *t*-tests (α=0.05).

A statistical model appropriate for a split-split plot experiment was used to determine the effect of thinning, crown zone and leaf age class on A_{max} (μmol m^{-2} s^{-1}), specific leaf area (m^2 g^{-1}), foliar N content (g m^{-2}), foliar P content (g m^{-2}), and nitrogen-use efficiency, A_{max}/N (μmol CO_2 s^{-1} g^{-1} N). Thinning treatment was the whole-plot factor and crown zone and leaf age classes were considered as sub-plot factors. An additional F-test was run in the model, with thinning treatment used as a hypothesis effect and tree used as an error term. Analyses were carried out using the GLM module of the SAS statistical software (SAS Institute Inc., Cary, NC, USA).

Total N and total P per tree at the beginning and at the end of the experiment were estimated using leaf area per zone and the mean N and P (on a leaf area basis) per

zone. N and P estimates for each zone were summed to give total tree N and P.

Differences in the change of leaf area between thinning treatments were explored using one-way ANOVA. The influence of thinning on leaf water potential was investigated using analysis of variance. The GLM module in SAS was used to analyse the data with respect to thinning treatment and tree.

8.3 Results

8.3.1 Light attenuation

The fraction of incident light (Q_f) declined with crown depth in both treatments. However, the attenuation of light was significantly greater in the unthinned treatment with a Q_f value of 0.09 at crown base, compared to a Q_f value of 0.44 in the thinned treatment ($p < 0.05$). While Q_f values for the upper crown zone were similar for both treatments, significantly higher Q_f values were found in the middle ($p < 0.05$) and lower ($p < 0.01$) crown zones of trees in the thinned treatment (Figure 8.1). For both treatments, the Q_f values at each crown position were not affected by aspect.

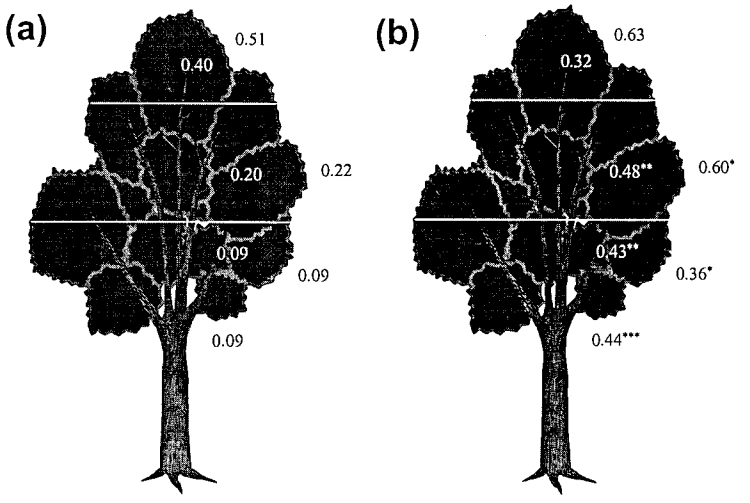


Figure 8.1 Distribution of the mean light fraction (Q_f) throughout the crowns of trees in (a) unthinned and (b) thinned treatments. Asterisks show significantly different Q_f between the two treatments ($p = 0.05$).

8.3.2 Light-saturated photosynthetic rate (A_{max})

Throughout the measurement period (which commenced 14 months post-thinning), the thinning treatment significantly increased A_{max} (Table 8.1; $p < 0.05$). The effect of leaf age class was highly significant throughout the experiment ($p < 0.01$). The smallest A_{max} values were measured in old foliage and the greatest were generally in apical foliage.

Greater A_{max} values were found in all leaf age classes in the lower crown zone of the thinned compared to the unthinned treatment throughout the growing season (Figure 8.2). In the middle crown zone, significantly higher A_{max} values in old foliage were found in the thinned treatment. A_{max} values of mature and apical foliage in this crown zone were higher in the thinned treatment for the last three measurement periods. In the upper crown zone, mature foliage of each thinning

treatment had similar A_{max} values throughout most of the measurement periods. The magnitude of the increase in A_{max} as a result of thinning increased during the course of the experiment and was always greatest in the lower and middle crown zones (data not shown). The general decline in A_{max} during the course of the experiment may have been caused by either low rainfall during this period (Figure 2.2) or declining temperatures (Table 8.2).

Table 8.1 Results from analysis of variance of A_{max} values measured at Creekton, 4 March 1999.

	df	MSS	F	*P*
Tree(Thin)	5	10.164	2.59	0.0295
Age	2	76.251	19.47	<0.0001
Thin*Age	2	10.640	2.72	0.0707
Zone*Age	3	6.493	1.66	0.1805
Thin*Zone*Age	2	4.464	1.14	0.3237
Test of hypotheses using MSS for Tree(Thin) as an error term				
Thin	1	129.928	12.78	0.0160
*Test of hypotheses using MSS for Tree*Zone(Thin) as an error term*				
Zone	2	41.944	8.77	0.0077
Thin*Zone	2	14.285	2.99	0.1013

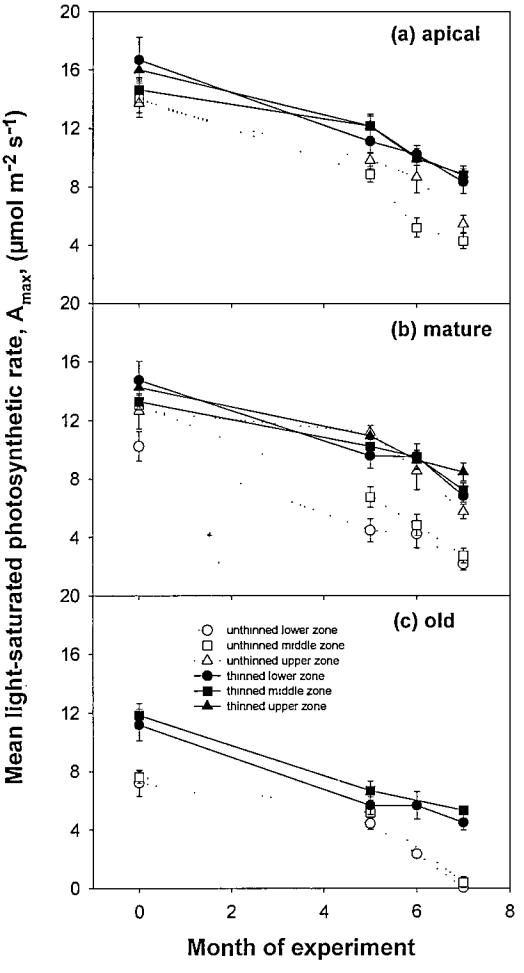


Figure 8.2 Mean light-saturated photosynthetic rate of (a) apical, (b) mature and (c) old foliage in the crowns of trees in thinned and unthinned treatments at Creekton from October 1998 to May 1999. Error bars show mean standard errors. Old foliage was measured in the lower and middle crown zones only. Old foliage in the middle zone of the unthinned treatment was not measured in the third measurement period.

Table 8.2 Maximum and minimum temperatures and relative humidity (RH) at the Creekton plantation for the two days of each measurement and the preceding day.

Date	Maximum temperature (°C)	Minimum temperature (°C)	Mean daily relative humidity (%)
14 October 1998	15.6	4.1	90.4
15 October 1998	15.9	5.3	76.3
16 October 1998	16.2	6.3	79.0
3 March 1999	21.8	13.4	100.0
4 March 1999	20.6	10.8	96.9
5 March 1999	21.0	9.4	99.1
21 April 1999*	11.2	5.1	84.0
22 April 1999*	13.5	4.4	70.0
23 April 1999*	13.9	0.9	86.0
17 May 1999*	14.7	5.5	86.0
18 May 1999*	12.8	6.7	78.0
19 May 1999*	17.5	6.6	93.0

*Meteorological data obtained from the Bureau of Meteorology weather station at Dover, 8 km from the Creekton experimental site. Relative humidity readings at 0900 AEST are given for each of these days.

8.3.3 Specific leaf area

Following thinning, the specific leaf area (SLA) of the trees in the thinned stand was significantly lower than that of trees in the unthinned stand ($p < 0.05$). SLA also decreased with increasing crown height for most of the measurement period ($p < 0.05$; Table 8.3). Crown zone had a significant effect on SLA ($p < 0.05$) with the highest values occurring in the lower crown zone and the lowest values in the upper crown zone.

Table 8.3 Distribution of specific leaf area ($m^2 g^{-1} \times 10^4$) by leaf age and crown zone for thinned (T) and unthinned (UT) treatments at Creekton. Mean standard errors are in parentheses.

Date	Crown zone	Old $m^2 g^{-1} \times 10^4$		Mature $m^2 g^{-1} \times 10^4$		Apical $m^2 g^{-1} \times 10^4$	
		UT	T	UT	T	UT	T
15 Oct 1998	lower	48.3 (1.3)	39.1 (1.1)	48.9 (1.3)	39.9 (1.8)	-	44.6 (0.0)
	middle	44.8 (0.0)	39.3 (1.2)	45.6 (1.7)	39.0 (1.0)	44.2 (2.3)	36.1 (1.5)
	upper	-	-	42.8 (1.3)	37.9 (1.0)	39.8 (2.2)	35.2 (0.8)
4 Mar 1999	lower	47.3 (3.1)	40.0 (0.8)	48.1 (2.7)	47.5 (5.2)	-	51.6 (4.2)
	middle	42.6 (0.0)	38.5 (0.9)	47.3 (3.8)	39.2 (1.5)	54.4 (6.5)	48.2 (0.9)
	upper	-	-	48.0 (2.6)	34.5 (1.3)	48.6 (2.5)	43.5 (3.0)
22 Apr 1999	lower	53.1 (0.9)	39.1 (0.1)	48.4 (1.0)	46.6 (1.8)	55.9 (0.0)	45.6 (1.5)
	middle	-	41.6 (4.1)	45.9 (1.4)	42.6 (3.0)	51.4 (4.4)	45.8 (2.4)
	upper	-	-	47.6 (3.8)	37.1 (2.2)	48.8 (2.4)	39.3 (2.3)
18 May 1999	lower	52.6 (1.0)	38.7 (0.3)	48.6 (2.3)	47.2 (2.0)	54.4 (1.6)	44.3 (0.3)
	middle	35.4 (0.0)	37.4 (1.3)	44.1 (2.6)	41.9 (3.1)	47.8 (2.6)	46.1 (2.2)
	upper	-	-	46.3 (1.9)	39.4 (3.5)	47.1 (2.2)	39.2 (1.4)

8.3.4 Foliar N content

Foliar nitrogen (N) content varied by thinning treatment and crown zone throughout the measurement period ($p < 0.05$). Foliar N content generally increased with crown height for both thinning treatments (Table 8.4). Foliar N concentrations on a dry weight basis were not affected by thinning treatment during the first three measurements, however thinning treatment was significant during the fourth measurement ($p < 0.05$).

When data from all leaf age and crown zone classes were pooled across periods, thinning improved the overall foliar N concentrations by 38 per cent. The decline in foliar N concentration from the apical foliage in the upper crown zone to the old foliage in the lower crown zone was greater in the unthinned treatment (46 per cent) than in the thinned treatment (19 per cent) when N concentrations were averaged across the measurement period.

8.3.5 Instantaneous N-use efficiency

Photosynthetic N-use efficiency (NUE) declined throughout the measurement period but did not vary between thinning treatments until the final measurement in May 1999 ($p < 0.05$). Leaf age had a significant effect on NUE ($p < 0.05$), but crown zone did not ($p > 0.05$). The greater NUE values were generally found in apical foliage, while the smaller values were found in old foliage (Table 8.5). The NUE of each thinning treatment declined throughout the growing season.

Table 8.4 Distribution of foliar N (g m^{-2}) by leaf age and crown zone for thinned (T) and unthinned (UT) treatments at Creekton. Standard errors are in parentheses.

Date	Crown zone	Old		Mature		Apical	
		UT	T	UT	T	UT	T
15 Oct 1998	lower	1.73 (0.13)	2.98 (0.30)	1.93 (0.12)	3.25 (0.16)	-	3.14 (0.00)
	middle	1.76 (0.00)	2.84 (0.27)	2.46 (0.04)	3.36 (0.24)	2.73 (0.07)	3.45 (0.06)
	upper	-	-	2.46 (0.01)	3.39 (0.27)	3.33 (0.14)	3.67 (0.10)
4 Mar 1999	lower	1.46 (0.02)	2.68 (0.24)	1.71 (0.17)	2.73 (0.04)	-	3.16 (0.15)
	middle	2.06 (0.00)	2.70 (0.13)	2.02 (0.14)	3.43 (0.68)	2.17 (0.16)	2.72 (0.15)
	upper	-	-	2.47 (0.18)	3.59 (0.38)	2.82 (0.04)	3.26 (0.28)
22 Apr 1999	lower	1.63 (0.02)	3.16 (0.25)	2.20 (0.04)	3.12 (0.10)	2.43 (0.00)	3.14 (0.17)
	middle	-	2.72 (0.24)	2.46 (0.19)	3.14 (0.16)	2.28 (0.05)	3.17 (0.22)
	upper	-	-	3.06 (0.16)	3.85 (0.28)	3.04 (0.25)	3.85 (0.32)
18 May 1999	lower	1.64 (0.29)	3.06 (0.16)	2.06 (0.01)	3.09 (0.10)	2.37 (0.01)	3.23 (0.09)
	middle	2.08 (0.00)	2.84 (0.22)	2.63 (0.19)	3.44 (0.28)	2.54 (0.07)	3.23 (0.12)
	upper	-	-	2.94 (0.26)	3.83 (0.41)	2.78 (0.14)	3.84 (0.27)

Table 8.5 Distribution of instantaneous nitrogen-use efficiency (NUE) (μmol CO_2 s^{-1} mol^{-1} N) by leaf age and crown zone for thinned and unthinned treatments at Creekton. Mean standard errors are in parentheses.

Date	Crown zone	Old		Mature		Apical	
		UT	T	UT	T	UT	T
15 Oct 1998	lower	57.9 (12.8)	52.7 (4.5)	73.6 (12.6)	63.8 (11.9)	-	74.3 (0.0)
	middle	60.5 (0.0)	56.9 (3.4)	74.5 (5.8)	55.9 (3.5)	72.2 (9.4)	59.1 (2.8)
	upper	-	-	71.7 (10.5)	59.7 (5.4)	57.7 (2.0)	61.2 (4.8)
4 Mar 1999	lower	42.3 (3.9)	30.1 (2.0)	32.4 (9.1)	49.1 (5.6)	-	49.4 (2.1)
	middle	35.0 (0.0)	34.9 (4.1)	47.7 (4.5)	42.5 (3.0)	58.2 (6.5)	63.5 (7.6)
	upper	-	-	63.2 (9.0)	43.7 (4.3)	49.0 (4.0)	50.8 (2.5)
22 Apr 1999	lower	20.1 (0.8)	25.2 (0.8)	26.7 (5.8)	42.7 (5.3)	30.5 (0.0)	45.8 (4.3)
	middle	-	41.4 (6.4)	28.6 (7.7)	42.9 (3.5)	32.3 (8.6)	44.8 (3.2)
	upper	-	-	39.1 (9.6)	33.8 (1.2)	39.0 (7.2)	36.3 (1.3)
18 May 1999	lower	0.5 (0.9)	20.6 (1.2)	15.3 (3.2)	31.1 (0.6)	19.8 (0.1)	36.2 (1.3)
	middle	2.7 (0.0)	26.3 (1.2)	15.1 (4.7)	29.9 (3.2)	23.8 (5.6)	38.2 (3.2)
	upper	-	-	27.3 (1.9)	31.1 (2.5)	27.1 (4.2)	33.1 (2.4)

A positive relationship between foliar N and A_{max} was found throughout the measurement period (eg. Figure 8.3). Similar relationships were observed for foliar N concentrations (Figure 8.3a) or foliar N content (Figure 8.3b). Figure 8.3 also shows the overall higher foliar N content of the thinned treatment. The relationship between foliar N and photosynthetic rate was best described by a quadratic function.

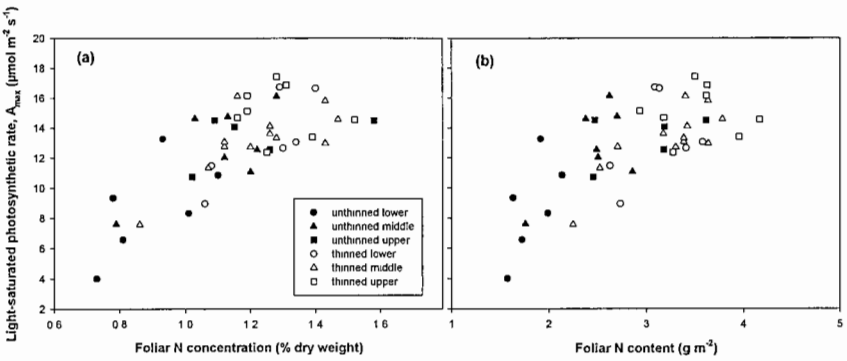
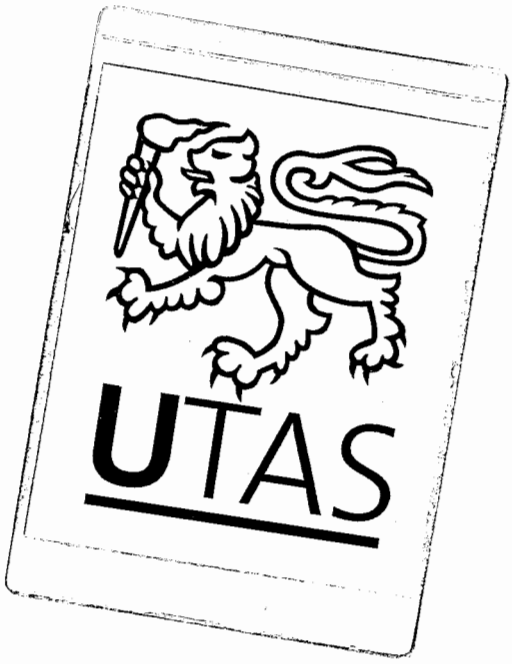


Figure 8.3 Relationships between light-saturated photosynthetic rate and (a) foliar nitrogen concentration and (b) foliar nitrogen content for thinned and unthinned trees by crown zone, 15 October 1998.

Combining the data for all treatments and canopy positions resulted in a positive relationship between foliar N concentration (Figure 8.4a) or content (Figure 8.4b) and mean fraction of incident light (see Figure 8.1).



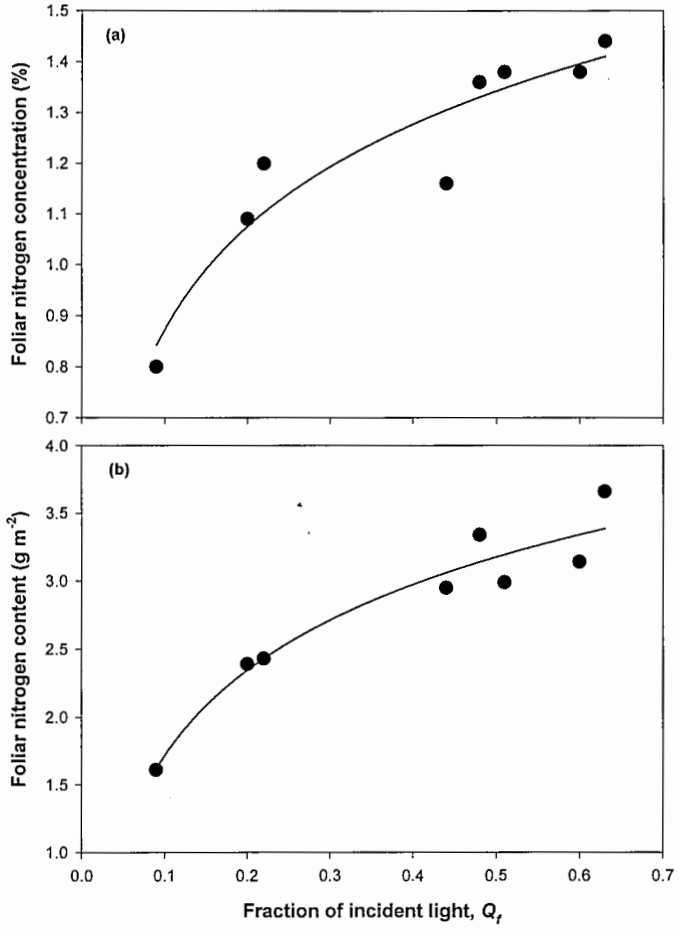


Figure 8.4 Relationship between light environment and (a) foliar nitrogen concentration and (b) foliar nitrogen content, at Creekton. Fitted lines are (a) $y = 1.55 + 0.29[Ln(x)]$, $r^2 = 0.87$, and (b) $y = 3.81 + 0.91[Ln(x)]$, $r^2 = 0.92$. Light fractions are values of Q_f throughout the crown (see Figure 8.1) and foliar N values are mean concentrations across the entire measurement period of the foliage age class best represented at each Q_f measurement position (either apical or mature). Data from thinned and unthinned treatments are pooled.

8.3.6 Foliar P content

Thinning treatment had a significant effect on foliar P content throughout the measurement period ($p < 0.05$; Table 8.6). Significant differences were found between crown zones ($p < 0.05$) with lowest foliar P content in the lower crown zone and highest foliar P content in the upper crown zone. Foliar P concentrations expressed on a dry weight basis were not affected by thinning. When data from all leaf age and crown zone classes were pooled across periods, thinning improved the overall foliar P content by 36 per cent. Both crown zone and leaf age had significant effects on foliar P content ($p < 0.001$). The highest foliar P content values for both treatments were in the apical foliage in the upper crown zone. The decline in P content with crown depth and leaf age was greater in the unthinned treatment (41 per cent) than the thinned treatment (17 per cent).

Table 8.6 Distribution of foliar P (g m^{-2}) by leaf age and crown zone for thinned and unthinned treatments at Creekton. Mean standard errors are in parentheses.

Date	Crown zone	Old		Mature		Apical	
		UT	T	UT	T	UT	T
15 Oct 1998	lower	0.11 (0.01)	0.19 (0.01)	0.13 (0.01)	0.20 (0.02)	-	0.20 (0.00)
	middle	0.10 (0.00)	0.18 (0.01)	0.15 (0.00)	0.21 (0.02)	0.16 (0.00)	0.22 (0.01)
	upper	-	-	0.15 (0.01)	0.21 (0.01)	0.19 (0.00)	0.21 (0.01)
4 Mar 1999	lower	0.09 (0.00)	0.17 (0.00)	0.11 (0.01)	0.18 (0.00)	-	0.20 (0.01)
	middle	0.12 (0.00)	0.15 (0.01)	0.13 (0.01)	0.20 (0.01)	0.15 (0.01)	0.21 (0.02)
	upper	-	-	0.16 (0.02)	0.21 (0.02)	0.18 (0.01)	0.22 (0.02)
22 Apr 1999	lower	0.12 (0.01)	0.19 (0.02)	0.13 (0.00)	0.19 (0.01)	0.18 (0.00)	0.20 (0.01)
	middle	-	0.17 (0.01)	0.14 (0.01)	0.19 (0.01)	0.15 (0.01)	0.21 (0.02)
	upper	-	-	0.17 (0.01)	0.22 (0.02)	0.20 (0.01)	0.23 (0.01)
18 May 1999	lower	0.12 (0.01)	0.18 (0.01)	0.13 (0.00)	0.19 (0.00)	0.16 (0.01)	0.19 (0.00)
	middle	0.11 (0.00)	0.17 (0.02)	0.15 (0.01)	0.20 (0.01)	0.15 (0.01)	0.20 (0.01)
	upper	-	-	0.17 (0.01)	0.22 (0.02)	0.17 (0.01)	0.22 (0.02)

A positive relationship between foliar P and A_{max} was found at low foliar P concentrations (< 0.07%; Figure 8.5a and < 0.16 g m^{-2}; Figure 8.5b) for the first three measurement periods. At higher P concentrations there was no relationship between foliar P and A_{max}.

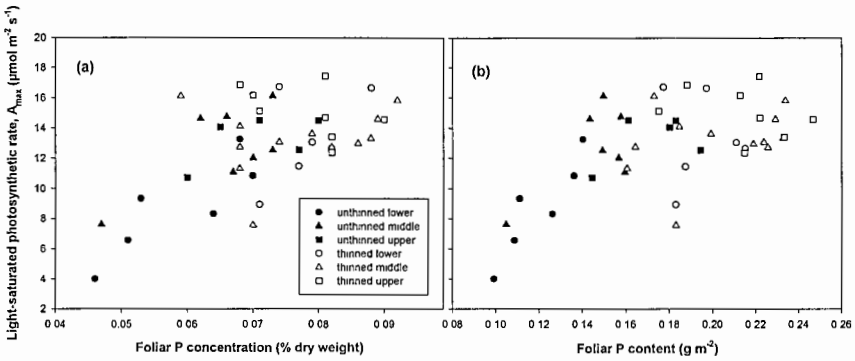


Figure 8.5 Relationships between light-saturated photosynthetic rate and foliar phosphorus concentration on a (a) dry weight and (b) leaf area basis for thinned and unthinned trees measured 15 October 1998.

Strong correlations were observed between foliar N concentrations and foliar P concentrations. Thinning treatment did not alter the nature of the relationship when expressed either on a leaf area basis (Figure 8.6a) or a leaf weight basis (Figure 8.6b).

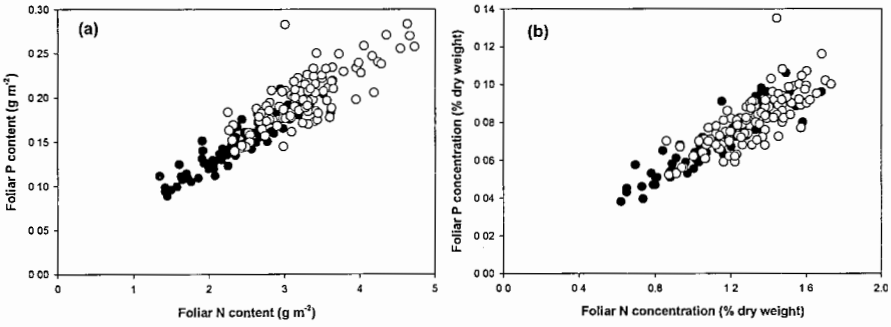


Figure 8.6 Relationship between foliar N and P concentrations for the thinned (○) and unthinned treatments (●). Data were pooled across all measurements.

8.3.7 Leaf area and nutrient levels

Over the course of the experiment, trees in the thinned and unthinned stands lost a similar proportion of leaf area from the lower crown zone and gained a similar proportion in the middle crown zone (Table 8.7). Overall, the relative increase in tree leaf area was greater in the thinned stand. However this could not be tested for statistical significance due to the small sample size. In October 1998 the number of branches in the lower crown zone was similar for each thinning treatment (4.7 branches per tree in thinned stand, 4.8 branches per tree in unthinned stand). During the course of the experiment there was senescence of 57% of branches in the lower crown zone of the thinned stand, and 44% of branches in the unthinned stand.

Table 8.7 Changes in mean leaf area per tree between October 1998 and June 1999 in thinned and unthinned treatments at Creekton. Crown zone positions were not altered from the October 1998 positions. Therefore the upper crown zone at June 1999 represents more than one-third of crown length because of tree height growth.

	Mean leaf area per tree (m^2)		
Crown zone	**October 1998**	**June 1999**	**% difference**
Thinned			
lower	17.1	11.8	-31
middle	36.3	39.6	+9
upper	18.0	35.6	+98
total	**71.4**	**87.0**	**+22**
Unthinned			
lower	12.7	8.2	-35
middle	16.5	17.5	+6
upper	3.0	8.4	+180
total	**32.2**	**34.1**	**+6**

The amount of nitrogen in the crowns of each tree in the thinned treatment increased by 28 per cent over the course of the experiment (Table 8.8). In the unthinned treatment, total nitrogen in each crown increased by 18 per cent. The

amount of phosphorus in the crowns of trees in the thinned treatment increased by 20 per cent. Phosphorus levels in the unthinned treatment increased by 14 per cent. The proportion of total crown nitrogen in the upper crown zone increased while that in the lower crown zone decreased for both thinning treatments.

Table 8.8 Mean total nitrogen and phosphorus content by crown zone for trees in thinned and unthinned treatments. For each crown zone, proportions of total crown nitrogen or phosphorus are given in parentheses.

Crown zone	Nitrogen content (g)		Phosphorus content (g)	
	Thinned	**Unthinned**	**Thinned**	**Unthinned**
		October 1998		
Lower	53.4 (0.23)	23.2 (0.33)	3.4 (0.23)	1.5 (0.35)
Middle	116.8 (0.50)	38.2 (0.55)	7.4 (0.51)	2.3 (0.53)
Upper	63.5 (0.27)	8.7 (0.12)	3.8 (0.26)	0.5 (0.12)
Total	**233.7**	**70.1**	**14.6**	**4.3**
		June 1999		
Lower	36.9 (0.12)	16.6 (0.20)	2.2 (0.13)	1.1 (0.22)
Middle	125.5 (0.42)	42.3 (0.51)	7.5 (0.43)	2.4 (0.49)
Upper	136.5 (0.46)	24.0 (0.29)	7.8 (0.44)	1.4 (0.29)
Total	**298.9**	**82.9**	**17.5**	**4.9**

8.3.8 Leaf water potential

Thinning had no effect on Ψ_{pd} eighteen months after the thinning treatment was imposed ($p > 0.05$). Creekton experienced very low rainfall during January prior to measurement (8 mm). However, the rainfall at Creekton during the three weeks immediately prior to Ψ_{pd} measurement was 158 mm. It is therefore unlikely that the trees were experiencing water stress at the time of Ψ_{pd} measurement. However, Ψ_{mid} of the thinned trees was significantly lower than that of the control trees ($p < 0.05$) despite variation between trees within each treatment.

Table 8.9 Mean pre-dawn (Ψpd) and midday (Ψmid) leaf water potential of trees from thinned and unthinned treatments at Creekton, measured 3 March 1999. Values in parentheses show ± one standard deviation.

	Thinned	Control
Ψ_{pd} (MPa)	-0.38 (0.05)	-0.40 (0.05)
Ψ_{mid} (MPa)	-1.14 (0.09)	-0.94 (0.12)

A set of diurnal Ψ_l measurements showed the effect of incident solar radiation on trees from thinned and unthinned treatments (Figure 8.7). While Ψ_l decreased in both thinned and unthinned treatments during a period of high incident solar radiation, the Ψ_l of trees from the thinned treatment was significantly lower than that of trees from the unthinned treatment ($p < 0.05$).

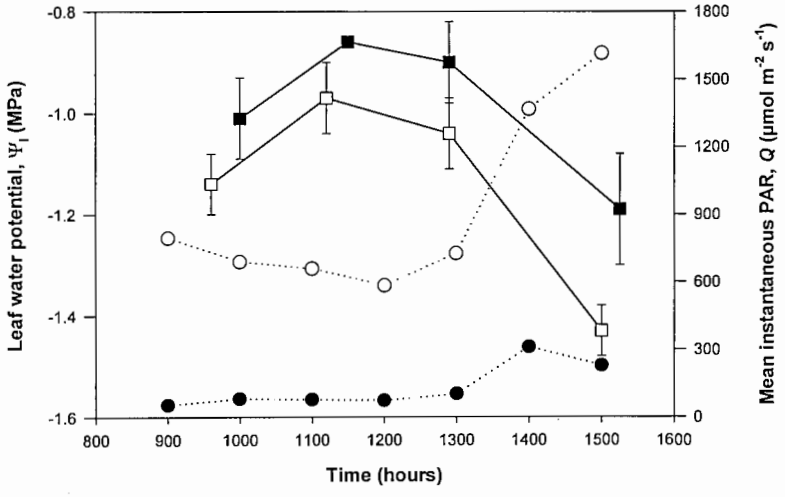


Figure 8.7 Mean leaf water potential of foliage in the lower crown of trees in thinned and unthinned treatments at Creekton during 21 January 1999. (❑=thinned, ■=unthinned, ○=hourly photosynthetically active radiation (PAR) above the canopy, ●=hourly PAR below the canopy of unthinned stand)

8.4 Discussion

8.4.1 Photosynthetic capacity

Photosynthetic rates under high intensity, constant light conditions (photosynthetic capacity, A_{max}) increased as a result of thinning during the 14 to 21 month period post-thinning. Maximum A_{max} values (*c.* 20 μmol m^{-2} s^{-1}) measured in this study were similar to the highest reported for *E. nitens* (Battaglia et al. 1996; Pinkard et al. 1998). The increases in A_{max} after thinning were due mainly to changes in the photosynthetic capacity of old and mature foliage in the lower and middle crown zones. These increases, combined with the improvement in light microenvironment, may be pivotal in driving the initial growth response to thinning in *E. nitens* stands. While an increase in A_{max} for a closed eucalypt canopy was shown to have little effect on growth (McMurtrie et al. 1989), a similar increase in stands after thinning, where a higher proportion of foliage experiences light-saturating conditions, would have a more pronounced effect on tree growth.

Improved photosynthetic capacity after thinning has been demonstrated in conifer species. For example, lower crown foliage of *P. taeda* had a similar photosynthetic capacity to that of upper crown foliage during the first year after thinning, while the lower crowns of trees in the unthinned stand had significantly lower photosynthetic capacity (Ginn et al. 1991). Measures of photosynthetic performance under ambient light conditions show increased rates in the lower crowns after thinning (Wang et al. 1995; Gravatt et al. 1997; Peterson et al. 1997; Tang et al. 1999). While actual photosynthetic rates throughout the crown are useful for estimating levels of photosynthate production, measures of

photosynthetic capacity (A_{max}) provide an indication of whether trees have greater ability to take advantage of the increased light after thinning. In this study the main increases in A_{max} occurred in the lower and middle sections of the crown. Thinning significantly altered the light environment of these areas of the crown, suggesting that light was limiting physiological activity in the crowns of this stand prior to thinning.

8.4.2 Foliar nutrient levels

Foliar P concentrations were similar to published values for *E. nitens* (Misra et al. 1998b; Pinkard et al. 1998) and *E. grandis* (Leuning et al. 1991a). However for the duration of the experiment, concentrations of both the thinned and unthinned treatments were below 0.13 % of dry weight, a level considered adequate for mature *E. nitens* (Judd et al. 1991; Boardman et al. 1997). Thinning improved the foliar N concentrations to levels above 1.33 % of dry weight. This concentration is given as a threshold by Boardman et al. (1997) for adequate nutrition for *E. nitens*. In contrast, the foliar N concentrations of the unthinned stand were generally below this level.

A gradient in foliar N concentration was measured in both the vertical (crown zones) and the horizontal (leaf age within crown zones) directions. A similar pattern was found in mature *P. contorta* stands (Schoettle and Smith 1999). For the mature and apical foliage in the present study, the differences in foliar N concentration between thinning treatment and leaf age were well explained by the light microenvironment, Q_f. As such, the data lends support to the nitrogen allocation theory that foliar N is distributed within the canopy according to the prevailing light environment (Field 1983; Givnish 1988; Evans 1989; Leuning et al. 1991a). While thinning has been found to generally improve foliar N

concentrations (Wang et al. 1995) and light microenvironment (Wang et al. 1995; Gravatt et al. 1997; Tang et al. 1999), the effect of thinning on the spatial nature of the relationship between foliar N and light has not previously been examined.

Dilution of foliar nutrients can occur in actively growing crowns. In a thinning study of *E. regnans*, Messina (1992) found higher foliar nitrogen concentrations in the thinned stand three months after thinning, yet 27 months after thinning nitrogen concentrations had declined to levels lower than that of foliage in the unthinned stand. Foliar levels of N and P did not differ significantly between thinned and unthinned treatments two years after thinning a *P. taeda* stand but the consistently lower levels in thinned stands suggested that dilution of nutrients may have occurred as a result of the greater growth (Ginn et al. 1991). Messina (1992) had also concluded that the temporal change in foliar nitrogen concentration was due to a dilution effect resulting from an expansion of crown biomass after thinning. In the present study, crown biomass in the thinned stand increased at a greater rate than in the unthinned stand (Table 8.7). This is consistent with other studies of changes in crown biomass following thinning (Beets and Pollock 1987; Ginn et al. 1991; Mitchell et al. 1996). Thus a longer-term response of *E. nitens* to thinning may be a decline in foliar nitrogen concentrations as crown biomass increases.

Both foliar nitrogen and phosphorus content were higher after thinning because thinning significantly lowered specific leaf area (SLA). Measures of SLA provide an indication of leaf thickness. A decrease in SLA (resulting in thicker leaves) may be due to an increase in the amount of photosynthetically active components in a given leaf area and consequently, an improved capacity to convert intercepted light into organic matter (Le Roux et al. 1999). The higher nutrient content found

after thinning is consistent with other studies that have shown that variation in nitrogen content is associated with variability in specific leaf area rather than in nitrogen concentration on a dry weight basis (Rosati et al. 1999; Wilson et al. 2000). Decreases in SLA with increasing irradiance levels have been shown for a wide range of trees species including *P. menziesii* (Bartelink 1996), *Fagus sylvatica* L. (Bartelink 1997) and *Quercus ilex* L. (Gratani 1997). The ability of *E. nitens* to lower SLA in the 12 months post-thinning indicates a high degree of plasticity in leaf morphology and a high adaptability in response to changes in light environment (Gratani 1997).

Thinning did not influence instantaneous leaf nitrogen-use efficiency (NUE) for most of the measurement period. Photosynthetic enhancement as a result of thinning was related to increases in foliar N concentrations, not to increases in NUE. This is despite evidence that NUE of *E. globulus* seedlings increases with increasing supply of N (Sheriff and Nambiar 1991). It also contrasts with Wang et al. (1995) who found an increase in both N concentrations and NUE in *B. papyifera* in the first two years following thinning. While the NUE values were within the range of NUEs of several eucalypt species (Mooney et al. 1978), they were less than those reported for *E. nitens* grown on a highly productive site (Pinkard et al. 1998) and similar to that of N-deficient *E. globulus* seedlings (Sheriff and Nambiar 1991). The decline in NUE with leaf age (Pinkard et al. 1998) may reflect a decrease in the amount of foliar N partitioned to a photosynthetic role or changes in the efficiency of carbon assimilation with senescence not associated with nutrition (Sheriff et al. 1995).

Increased nutrient availability can increase productivity if the nutrient in question is limiting carbon gain (Sheriff 1996). Nitrogen can have a large impact on carbon

assimilation as it is an essential component of chlorophylls and thylakoid proteins (Raven et al. 1986). Positive correlations between foliar N concentration (either leaf area or dry weight) and photosynthetic capacity have been shown for eucalypt species (eg. Leuning et al. 1991a; Sheriff and Nambiar 1991; Sheriff 1992) as well as for other tree genera (eg. Walters and Reich 1989; Sheriff and Mattay 1995; Schoettle and Smith 1999; Kazda et al. 2000). But there are instances where no relationship has been found (eg. Sheriff 1995; Pinkard et al. 1998) indicating that A_{max} may have been more limited by other factors in these studies. In the present study A_{max} was positively correlated with N concentrations up to *c.* 1.2 % or between 2.5 and 3.0 g m^{-2}. In Figure 8.3, A_{max} at these concentrations was *c.* 14 μmol m^{-2} s^{-1}, a value similar to 12.2 μmol m^{-2} s^{-1} found for *E. globulus* seedlings (Sheriff and Nambiar 1991). At greater N content A_{max} increased at a slower rate with increasing N, indicating that N content was not limiting A_{max}. At these high foliar N content values, A_{max} is likely to be limited by physical resistances to CO_2 diffusion into the leaf and the resulting constraint on internal CO_2 pressure (Sheriff and Nambiar 1991). The increase in foliar N content in *E. nitens* after thinning meant that A_{max} was not limited by N availability throughout the experiment.

A_{max} was positively correlated with foliar P content. However foliar N and P concentrations were correlated in this study (Figure 8.6), making it difficult to establish if A_{max} was directly dependent on P content. When P was applied as the only limiting nutrient in a glasshouse experiment with *E. grandis* seedlings, a positive relationship between A_{max} and P was found (Kirschbaum and Tompkins 1990). A positive correlation was also found in *P. radiata* (Sheriff et al. 1986; Sheriff 1995). The A_{max} of *E. grandis*, *E. pilularis* Smith, and *E. gumifera* (Sol. ex

Gaertner) Hochr. seedlings was not limited by foliar P concentrations greater than 0.02 % (Mulligan 1989). A suggested threshold concentration of 0.07 % (Leuning et al. 1991a) was supported by the findings of this study (Figure 8.5a). At concentrations below 0.07 % in *E. nitens* A_{max} may be limited by low rates of ATP and NADPH formation (Mulligan 1989). At levels above 0.07 % where A_{max} was not correlated with foliar P concentration, the additional P may be stored in cell vacuoles and not directly involved with photosynthetic reactions (Kirschbaum and Tompkins 1990).

8.4.3 Leaf area dynamics

While total leaf area of the trees in the thinned stands increased at a higher rate, a similar proportion of leaf area in the lower crown zone was lost as for trees in the unthinned stand (Table 8.7). This was despite the improvement in irradiance of the lower crown after thinning. The reasons for this are not apparent but may be due to errors in the procedure for estimating leaf area from branch cross-sectional area. During the course of the experiment, qualitative observations were made of the presence of apical foliage in the lower crown of trees in the thinned stand. Branches in the lower crown of post-canopy closure *E. nitens* carry a smaller amount of leaf area for a given branch size (see Table 4.3) due to leaf senescence. It is suggested that that thinning rejuvenates branches in the lower crown but that any initial increase in leaf area was not matched by a corresponding increase in branch size. In the longer term the leaf area of the lower crown of *E. nitens* is expected to increase as a result of thinning (Chapter 6).

8.5 Conclusions

The ability to isolate a single mechanism driving improved growth after thinning

is complicated by simultaneous changes in relationships between photosynthesis, light and nutrients (Schoettle and Smith 1999) as well as increases in tree water use (Nambiar et al. 1984). While enhanced A_{max} was positively associated with improvement in irradiance conditions and increases in nitrogen and phosphorus concentration following thinning, the changes in nutrient concentration were due to decreases in specific leaf area. As specific leaf area decreases with increasing irradiance (Le Roux et al. 1999), changes in the physiological performance of *E. nitens* following thinning are likely to be primarily driven by the significant improvement in light availability. A similar conclusion has been reached in studies of conifer tree species (Gravatt et al. 1997; Peterson et al. 1997; Tang et al. 1999). The enhanced A_{max} after thinning may be a short-term response only. Enhanced A_{max} in *P. taeda* was found three years after thinning (Nowak et al. 1990; Ginn et al. 1991), but not five years after thinning (Gravatt et al. 1997). While higher nitrogen and phosphorus content and enhanced A_{max} are short-term responses to thinning in *E. nitens*, in the longer-term the increase in crown biomass after thinning (see chapters 4 and 6) may drive higher growth rates. In the following chapter, the impact of thinning-induced physiological changes in terms of stem biomass production is explored using a modelling approach.

Chapter 9. The physiological basis for thinning *E. nitens*: a modelling analysis

9.1 Introduction

Forest managers are interested in predicting tree and stand responses to thinning in terms of stand production and stem growth. In many cases this is achieved through the use of mensurational models based on measurements from a range of sites and treatments (eg. Candy 1997). While such models are useful management tools, they are essentially non-transportable – that is, they cannot be confidently applied to site conditions and/or silvicultural treatments that extend beyond the suite of sites and treatments used to construct the model (Landsberg and McMurtie 1985; Linder 1985; Battaglia and Sands 1998).

Mechanistic or process-based models are able to overcome this limitation as predictions are based on physiological processes that control growth and the effect the environment has on these processes (eg. West 1993; Landsberg and Hingston 1996). Relatively simple mechanistic models have potential as powerful management tools as modelling stand dynamics under a range of thinning strategies can substitute for lengthy field experiments (Courbaud 2000).

Process-based models of tree growth generally require an understanding of the changes in dynamics of light interception and use by the canopy (Linder et al. 1985; Wang and Jarvis 1990; Landsberg and Hingston 1996; Bartelink 1998a) and the effect of growing conditions and functional balances on dry matter partitioning between tree components (Mäkelä 1986; West 1993; Cannell and Dewar 1994; Bartelink 1998b). Thinning of *E. nitens* plantations can improve the

growth rate of retained trees (Chapter 3, Gerrand et al. 1997a,b; Stackpole et al. 1999). The significant improvements in the light environment and photosynthetic capacity of the crown (Chapter 8) are likely to causes changes in light interception and light-use efficiency. In addition, changes in tree structure with growth rate (Chapter 4) that include altered branch size and leaf area distribution (Chapter 6) suggest changes in partitioning of biomass as a result of thinning. In this chapter, a simple modelling approach was used to determine the effect of thinning on growth and biomass partitioning. The relative importance of the physical and physiological changes after thinning was investigated by considering growth as a function of independent factors and investigating the effect of thinning on each factor (eg. Medlyn 1996). The net change in stem biomass with time (ΔW_s) can be modelled using the light-use efficiency approach (see review by Cannell 1989a). This approach incorporates light interception by modelling the attenuation of photosynthetically active radiation (PAR) with canopy depth using Beer's law (Sands 1995), the efficiency of converting PAR to biomass, and the patterns of carbon allocation by;

$$\Delta W_s = \eta_s \varepsilon Q_o (1 - e^{-kL}) \qquad 9.1$$

where η_s is the stem partitioning of net biomass, ε is the net photosynthetic light use efficiency of the canopy, Q_o is incident PAR, k is the light extinction coefficient, and L is leaf area index. Beer's law can be applied to continuous canopies but is less valid for a discontinuous canopy. The effect of a discontinuous canopy produced by thinning can be overcome by including F, a simple canopy fraction factor calculated as the ratio of projected canopy area to

ground area;

$$\Delta W_{s,tree} = \eta_s \varepsilon Q_o (1 - e^{-k\frac{L}{F}}) \qquad 9.2$$

where $\Delta W_{s,tree}$ is the stem biomass production per tree. Equation 9.2 allows the effects of thinning to be separated into the effects on photosynthetic rates (*ie.* effect on ε), leaf area (*ie.* effects on F and L) and biomass partitioning (*ie.* effect on η_s). The light-use efficiency approach has been used to study growth of *E. globulus* (Linder et al. 1985; Landsberg and Hingston 1996) and the effect of atmospheric carbon dioxide and leaf nitrogen concentrations on growth of *P. radiata*, *Nothofagus fusca* (Hook. f.) Ørst and *E. grandis* (Medlyn 1996). In the present study, data from an unthinned *E. nitens* stand and from a stand thinned to 250 trees ha^{-1} were used to examine the extent to which thinning alters the various parameters of equation 9.2 and to gauge the influence of such changes on stem biomass production.

9.2 Methods

9.2.1 Light interception

Interception of photosynthetically-active radiation (PAR) by the crowns of *E. nitens* in unthinned and 250 trees ha^{-1} stands was calculated from PAR measurements at various positions in the crown. The method used to measure PAR is described in Chapter 8. The PAR environment of two trees from each of the unthinned and 250 trees ha^{-1} treatments were measured during the summer of 1998/99. For each tree, daily incident PAR (Q_o) was calculated from a clear day

from both the northern and southern measurement periods. At solar noon and for the preceding and following hour, intercepted PAR (Q_i) was calculated as

$$Q_i = Q_o - Q_{cb} \qquad 9.3$$

where Q_{cb} was the mean of the southern and northern readings at crown base.

To incorporate PAR interception by the crown at lower solar angles during the remaining hours, the incident PAR at the southern middle crown zone ($Q_{o,s,mid}$) was subtracted from the incident PAR at the northern upper crown zone ($Q_{o,n,upp}$). In addition, the incident PAR at the southern lower crown zone ($Q_{o,s,low}$) was subtracted from the incident PAR at the northern middle crown zone ($Q_{o,n,mid}$). Total PAR interception was then calculated as;

$$Q_i = (Q_o - Q_{cb}) + (Q_{o,n,upp} - Q_{o,s,mid}) + (Q_{o,n,mid} - Q_{o,s,low}) \qquad 9.4$$

The product of Q_i and crown projection area was used as total crown PAR interception. Crown projection area per tree in each treatment was calculated using crown width measurements made on all scaffolding trees (see Chapter 8 for explanation of scaffolding) in June 1999.

9.2.2 Above-ground biomass production

Annual stem biomass production for trees in the 250 trees ha^{-1} and unthinned treatments were calculated using diameter and height measurements at 12 and 24 months post-thinning treatment. Stem volume was calculated using the volume function of Opie (1976). Stem mass was calculated using a wood density of 460 kg m^{-3} (Yang and Waugh 1996).

Annual foliage production by trees in the two thinning treatments was calculated using measurements from a LAI-2000 Plant Canopy Analyser (Li-cor Inc.,

Lincoln, Nebraska, USA) made six and 18 months post-thinning (see Chapter 6 for details). Leaf areas were converted to leaf mass using a mean specific leaf area (SLA) value calculated from all crown zones, foliage age classes and measurement periods (see Chapter 8). A separate SLA value was calculated for the 250 trees ha^{-1} and unthinned treatments.

Annual branch production per tree was estimated from branch diameters measured on all scaffolding trees in October 1998 and June 1999. Branch fresh weights were estimated using a single relationship between branch diameter and weight established for fertilized and unfertilized *E. nitens* plantation trees (Spurr, unpublished data). Branch weights were summed to give branch weight per tree.

9.2.3 Respiration

In the absence of specific relationships for plantation eucalypts, above-ground maintenance respiration (R_m) was estimated using relationships established for *P. radiata* (Ryan et al. 1996).

Branch R_m is proportional to branch volume (Ryan et al. 1996). To calculate branch R_m , branch weights of each scaffolding tree (see above) were converted to volume using a wood density of 460 kg m^{-3} (Yang and Waugh 1996). Branch volumes of the upper and middle, and the lower crown zones were summed separately to use the equations of Ryan et al. (1996).

Foliage R_m is directly proportional to foliar nitrogen (N) concentration (Ryan et al. 1996). For each treatment, mean foliar N concentration was calculated using data from all crown zones, foliage age classes and measurement periods (see Chapter 8 for details).

Stem R_m is proportional to stem sapwood volume (Ryan et al. 1996). Six trees that

had been destructively sampled from the Creekton plantation prior to thinning treatment (see Chapter 5 for details of CK-F) were used to determine the relationship between stem size and sapwood volume. For each sampled tree, sapwood volume was estimated using the sapwood area values at established stem heights and the method of Ryan (1989). Sapwood volume (m^3) could be predicted from stem basal area (m^2) using;

$$y = 3.80x \qquad (n=6, r^2=0.99) \qquad 9.5$$

This equation was used to estimate the sapwood volume of each scaffolding tree for June 1999.

9.2.4 Turnover

Branch biomass turnover rate was assumed to be proportional to the rate of crown lift. The mean annual lift in crown base was calculated from measurement of crown base height, six and 18 months post-thinning. The crown base height rose by a similar proportion for both thinning treatments (0.10). This proportion was applied to the branch biomass at June 1999 of each scaffolding tree to estimate branch turnover rate.

In the absence of published data on leaf longevity in *E. nitens*, annual foliage biomass turnover was assumed to be 0.33 (as per Battaglia and Sands 1997) of standing foliage biomass and independent of stand density.

9.3 Results

9.3.1 Light interception

For the days used in the analysis (clear days during December and January), mean daily incident PAR was 11.5 MJ m^{-2} d^{-1}. Based on the conversion of Sands

(1995), total daily incident radiation was 23 MJ m^{-2} d^{-1}. Thinning to 250 trees ha^{-1} increased the level of intercepted PAR by the retained crowns by 96 per cent (Table 9.1).

Table 9.1 The effect of thinning on photosynthetically-active radiation (PAR) interception by tree crowns.

Thinning treatment	Intercepted PAR		Mean crown projected area	Intercepted PAR per crown
	MJ m^{-2} d^{-1}	MJ m^{-2} a^{-1}	m^2	MJ $tree^{-1}$ a^{-1}
250 trees ha^{-1}	10.7	3906	10.9	42570
unthinned	8.9	3249	6.7	21765

9.3.2 Above-ground biomass partitioning

Thinning altered the pattern of biomass partitioning by increasing the partitioning (NPP) to branches at the expense of stem wood (Table 9.2). Partitioning of gross primary production (GPP), where respiration and turnover levels are included, shows a greater partitioning to foliage, reflecting its high respiratory cost.

Table 9.2 Above-ground biomass partitioning between stems, foliage and branches for 250 trees ha^{-1} and unthinned treatments.

Thinning treatment	Stem partitioning η_s	Foliage partitioning η_f	Branch partitioning η_{br}
		Partitioning of NPP	
250 trees ha^{-1}	0.78	0.13	0.09
unthinned	0.87	0.12	0.01
		Partitioning of GPP	
250 trees ha^{-1}	0.45	0.42	0.13
unthinned	0.31	0.63	0.06

9.3.3 Light-use efficiency

Light-use efficiency (ε) describes the efficiency with which trees convert intercepted light to biomass via photosynthetic pathways. For each thinning

treatment, ε was calculated on an annual basis using the intercepted light per crown (Table 9.1) converted to total radiation using Sands (1995) and annual above-ground biomass production per tree. The value of ε increased by 29 per cent as a result of thinning. Trees in the unthinned stand had an ε value of 0.31 g MJ^{-1}. The ε value of trees in the 250 trees ha^{-1} stand was 0.40 g MJ^{-1}.

9.3.4 Respiration and turnover

For both thinning treatments, maintenance respiration (R_m) of foliage represented the greatest proportion of total tree above-ground R_m (75 per cent in 250 trees ha^{-1} treatment, 80 per cent in unthinned treatment, Table 9.3). Branch R_m was greater than stem R_m in the 250 trees ha^{-1} treatment, but similar in the unthinned treatment (Table 9.3). On a per tree basis, total R_m was 98 per cent greater in the 250 trees ha^{-1} treatment when compared with the unthinned treatment. On a per hectare basis however, the total R_m of the unthinned treatment was 125 per cent greater than the 250 trees ha^{-1} treatment. R_m for branches, foliage and stem were 4.44, 23.68 and 3.24 μmol s^{-1} $tree^{-1}$, respectively, in the 250 trees ha^{-1} treatment and 1.50, 12.72 and 1.63 μmol s^{-1} $tree^{-1}$, respectively, in the unthinned treatment.

The increase in branch and foliage weight per tree in the 250 trees ha^{-1} treatment ensured that turnover rates were 140 and 63 per cent greater, respectively, than that of trees in the unthinned stand. Total annual biomass turnover rates were estimated as 7.2 kg $tree^{-1}$ a^{-1} in the 250 trees ha^{-1} treatment and 4.0 kg $tree^{-1}$ a^{-1} in the unthinned treatment.

R_m and turnover combined were estimated to make up 53 per cent of GPP in the 250 trees ha^{-1} treatment. In the unthinned treatment, R_m and turnover comprised 32 per cent of GPP.

Table 9.3 Maintenance respiration rates on a per tree and per stand basis for the 250 trees ha^{-1} and unthinned treatments. (DM = dry matter)

Thinning treatment	Annual R_m (kg DM tree^{-1} a^{-1})			Annual tree R_m kg DM tree^{-1} a^{-1}	Annual stand R_m t DM ha^{-1} a^{-1}
	Branch	Foliage	Stem		
250 trees ha^{-1}	4.2	22.4	3.1	29.7	7.5
unthinned	1.4	12.0	1.5	15.0	16.9

9.3.5 Above-ground stem biomass production

The calculated values of η_s, ε, and Q_i can be used to predict stem biomass production using the format of equation 9.1.

For the unthinned treatment, predicted annual stem biomass production was 11.8 kg tree^{-1} a^{-1}. This result was similar to actual stem biomass production, measured as 12.0 kg tree^{-1} a^{-1}. For the 250 trees ha^{-1} treatment, predicted annual stem biomass production was 26.8 kg tree^{-1} a^{-1}. This underestimated actual production by 17 per cent (measured stem biomass production was 32.4 kg tree^{-1} a^{-1}).

9.4 Discussion

9.4.1 Light interception

The annual amount of light intercepted by a canopy is dependent to a large extent on leaf area and canopy structure (Jarvis and Leverenz 1983). As a discontinuous canopy by virtue of thinning, the 250 trees ha^{-1} stand in this study intercepted less light than the unthinned stand. Based on a canopy projection area of 0.27 and the intercepted light values of Table 9.1, as a stand, the 250 trees ha^{-1} treatment intercepted 68 per cent less light than the unthinned stand. However, a tree in the 250 trees ha^{-1} stand intercepted more light than a tree in the unthinned stand due to a wider crown and reduced side shading. In the short-term, the reduction in side

shading by thinning has a large influence on the increase in intercepted light by retained crowns. In the 250 trees ha^{-1} stand, crown light interception per retained tree was almost double that of the unthinned stand, despite the mean leaf area of trees in the 250 trees ha^{-1} stand being only 39 per cent greater (60 m^2 versus 43 m^2). The 96 per cent increase in crown light interception after thinning was similar to that reported for *Abies balsamea* (L) Mill in the second year after thinning (Pothier and Margolis 1991). In the longer-term the difference in intercepted light is expected to increase as the crown projection area and leaf area of trees in the 250 trees ha^{-1} stand increases.

For a given value of light-use efficiency (ε), net annual biomass production has been shown to be linearly related to annual intercepted light (Linder 1985; Beadle and Inions 1990). Differences in ε aside, such a relationship can provide a rationale for reduced stand growth yet increased tree growth observed after thinning *E. nitens* stands (Chapter 3). At a stand level thinning decreases canopy light interception and reduced stand growth is expected. On a per tree basis thinning increases crown light interception and greater biomass production is expected.

9.4.2 Biomass partitioning

Given the strong relationship between biomass production and intercepted light (see above), a strategy that maximises the rate of crown development by increasing crown projection area and leaf area in theory should yield the greatest biomass production. In young unthinned *E. nitens* plantations, the partitioning of dry matter to branches gradually declines while the partitioning to stems increases (Beadle and Inions 1990). In this study, (12 to 24 months post-thinning), patterns of above-ground biomass partitioning were altered as a result of thinning. The

proportion of net above-ground biomass production assigned to branches increased as a result of thinning. This contrasts with Beets and Pollock (1987) who found above-ground partitioning in *P. radiata* plantations was not affected by early-age thinning. However Santantonio (1989) reported a decrease in partitioning of total biomass production to stem in *P. radiata* as a result of thinning.

The difference in branch partitioning between the two treatments was large. The greater branch partitioning in the thinned treatment may provide important benefits in terms of crown projection area. Branch diameter is strongly and linearly related to branch length (Medhurst, unpublished data). Thus, increases in branch growth after thinning will result in increased crown projection area, with benefits in terms of crown light interception. This is supported by observations of larger branches in the lower crown as a result of thinning (see Chapter 6) and by planting eucalypt species in isolation as opposed to regular plantation spacings (Henskens, unpublished data).

9.4.3 Light-use efficiency

Light-use efficiency (ε) is sensitive to environmental stress, such as water availability, nitrogen (N) availability and temperature (Jarvis and Leverenz 1983). Thinning increased ε in this study, suggesting that environmental stress was alleviated as a result of thinning and increased production was not solely due to greater light interception. The ε values obtained for both thinning treatments could be considered as low when compared with other ε values obtained for eucalypt plantations (eg. 0.90 g MJ-1 for E. globulus, Linder 1985). However, the ε values obtained for Creekton were similar to that of a nearby eucalypt plantation (0.45 g

MJ-1, Beadle et al. 1995). Low ε values indicate that environmental factors were limiting light utilization of the trees in the Creekton plantation. Greater transpiration rates per unit leaf area were measured in trees following thinning (see Chapter 7). In previous studies, thinning has been shown to have a positive effect on soil water availability (Cregg et al. 1990) and plant water status (Donner and Running 1986). The higher rates of water use at Creekton indicate a reduction in mild water stress during the growing season at this site which may have improved ε. A measured increase in foliar N concentrations as a result of thinning (see Chapter 8) would also improve ε. The theoretical dependence of ε on foliar N concentration has been demonstrated (Sands 1996). In all likelihood, the increase in ε after thinning at Creekton was due to a combination of improved water and N availability.

Any reduction in the partitioning of dry matter to roots as a result of thinning will also improve ε. Changes in the partitioning between above- and below-ground components were not considered as part of this analysis. However, the increase in soil water and nutrient availability after thinning may reduce the root:shoot ratio in the longer-term. For example, Axelsson and Axelsson (1986) suggested that a decrease in allocation of photosynthate to fine root production by well-fertilized trees was an important factor contributing to increased shoot growth.

9.4.4 Respiration and turnover

On the basis of twelve months growth, the proportion of above-ground GPP constituting maintenance respiration (R_m) and turnover was estimated to be greater as a result of thinning. Construction respiration (R_c) was not considered in this analysis as it is a fixed cost per unit dry matter built and is not directly influenced

by environmental differences (Ryan 1990). Greater R_m of stems following thinning measured by Lavigne (1988) and predicted in this analysis are due to larger sapwood volumes by virtue of their larger stem size (Ryan 1990). However as R_m varies strongly with temperature (Ryan et al. 1995), the R_m of trees in a thinned stand would be expected to be higher for a given sapwood volume. Given this, there is evidence that acclimation of stems to new temperature regimes following thinning may reduce the effect of greater temperatures on stem R_m (Lavigne 1987). If such acclimation occurs, the magnitude of the increase in R_m of stems and branches after thinning may be diminshed.

High foliage R_m per tree after thinning reflected both the greater leaf areas of trees in the 250 trees ha^{-1} treatment (average of 60 m^2 $tree^{-1}$ versus 43 m^2 $tree^{-1}$ in the unthinned stand) and the greater foliar nitrogen concentrations in the 250 trees ha^{-1} treatment (average of 1.31 % dry weight versus 1.12 % dry weight in unthinned stand). The increase in biomass partitioning to branches after thinning increased branch R_m per tree in the 250 trees ha^{-1} treatment. While R_m of woody tissue is low in comparison with that of foliage, R_m of branches is greater than that of large stems because of a greater component of living cells. R_m of trees after thinning is therefore expected to increase due to the greater investment in branches over stems.

For the purpose of this analysis a constant turnover rate of branches and foliage was assumed for both thinning treatments. However, thinning treatment may reduce biomass turnover if branch senescence is delayed. In the long-term, crown length increases after thinning (see Chapter 3) as lower branches are retained. In addition, the higher foliar nutrient concentrations in the 250 trees ha^{-1} treatment may increase leaf longevity. These changes would be expected to decrease branch

and foliage turnover rates after thinning.

9.5 Conclusions

The use of a simple light-use efficiency model to analyse the growth response to thinning provided a means of examining the effect of thinning on factors constraining growth in *E. nitens*. Considering stem biomass production in terms of crown intercepted light, net light-use efficiency and partitioning of biomass to stem wood highlighted the importance of crown dynamics in determining growth response to thinning.

Increased tree biomass production after thinning was driven by increases in both the level of intercepted light and the efficiency with which light energy was converted to biomass. When compared with trees from an unthinned stand, the proportional increase in intercepted light as a result of thinning was greater than the proportional increase in light-use efficiency. This suggests that the strategy of increased biomass partitioning to crown development after thinning plays an important role in driving the growth response. In plantations where growth is limited by water or nutrient availability, thinning is expected to improve the photosynthetic efficiency of the retained trees. However, in all plantations, the crown size at time of thinning and the rate of leaf area development after thinning will largely determine the magnitude and duration of stem growth response.

In addition, the rate of recovery of stand production following thinning will be related to the rate of return to canopy closure. However, the higher level of branch R_m may reduce overall production following canopy closure unless the increases in ε persist. This is unlikely if L returns to pre-thinning levels and water and nutrients again become limiting to growth.

Chapter 10. A review of thinning response and implications for *E. nitens* sawlog plantations

10.1 Introduction

A thinning regime should be a systematic plan for a whole rotation based on deliberate decisions about the kind of vegetation, benefits, and products desired (Smith 1986). The myriad of options for thinning regimes in *E. nitens* plantations can at first appear daunting. However, the viable options can be reduced to a more manageable number by consideration of the biological limitations to growth and the economic consequences of any decision. This thesis has considered the biological response of *E. nitens* to a range of thinning options. While an economic analysis was not carried out as part of this thesis, the ability to maintain rapidly growing trees through timely and adequate intervention by thinning will undoubtedly have a positive impact on any economic analysis.

The usefulness of understanding physiological responses to cultural treatment has been demonstrated with the development of site-specific pruning prescriptions for *E. nitens* stands (Pinkard 1997; Forestry Tasmania 1999). In this chapter, the growth response of *E. nitens* to thinning is considered in a physiological context. The implications these responses have for managers of eucalypt plantation estates are discussed.

10.2 Summary of results

10.2.1 Growth (chapter 3)

Using three trials that differed in respect to site quality, age at thinning and intensity of thinning, growth responses of *E. nitens* to thinning were examined. Individual tree growth was improved with increasing intensity of thinning so that the lowest stand density had the fastest individual tree growth. In terms of stand growth, very high intensity thinning (> 66 per cent of standing basal area) significantly reduced stand growth. Lower site quality appeared to affect the ability of a stand to respond to thinning when the first thinning operation was delayed until beyond canopy closure.

10.2.2 Allometry (chapters 4 and 5)

A study of trees from thinned and unthinned stands examined the functional relationship between stem sapwood area and crown leaf area. While thinning *per se* did not affect this relationship, the larger, faster growing trees had a higher leaf area:sapwood area ratio than the smaller trees in the study. Improved hydraulic conductivity of the sapwood in the larger trees was linked to the higher leaf area:sapwood area ratios. To further explore the significance of these relationships in *E. nitens*, a data set, consisting of 81 trees sampled from 13 post-canopy closure sites and 34 trees sampled from 6 pre-canopy closure sites, was used to examine the generality of allometric relationships for the species. The range of plantations from which the trees were sampled differed in site quality, stand age, fertiliser treatment, stand density and degree of weed infestation. Pre-canopy closure trees exhibited site-specific relationships that were to some extent confounded with tree age. However, post-canopy closure trees had relationships that were independent of site, age and silvicultural treatments. Strong

relationships between structural components were found for both stem and crown. Stem diameter at breast height was non-linearly related to tree height and crown length. Stem sapwood area (breast height or crown base) could be predicted from stem cross-sectional area. For post-canopy closure trees, a functional relationship between sapwood area (breast height and crown base) and leaf area was independent of site.

10.2.3 Crown development (chapter 6)

The crown structure of *E. nitens* six years after thinning and the development of stand leaf area index (L) both immediately and six years after thinning were investigated. Thinning did not alter branch angle, branching density or the relationship between branch size and branch leaf area. However, larger branches were found in the lower crown of trees after thinning and an increase in leaf area as a result of thinning occurred on the northern aspect of the crown. In unthinned stands the vertical distribution of leaf area was skewed towards the top of the crown and was correlated with live crown ratio. The vertical distribution of leaf area of trees in the thinned stand tended to be less skewed and was unrelated to tree size or dominance. L, as estimated from light interception measurements, increased at a constant rate soon after thinning regardless of residual stocking. In the longer term residual stocking had a strong influence on leaf area increase per tree and was correlated with changes in crown length.

10.2.4 Water use (chapter 7)

The water use of trees increased soon after thinning. Greater levels of water use were driven by changes in the radial distribution of sap flow across the sapwood. The conductivity of the inner sapwood increased and allowed greater water flow.

This resulted in a proportionally higher stand water use across the range of thinning treatments. During the 84-day measurement period, stand water use of the 100, 250, 600 and 1250 (unthinned) trees ha^{-1} treatments were, respectively, 50, 84, 118 and 218 mm. The higher individual tree water use meant, for example, that reducing stand density by 80 per cent (250 trees ha^{-1} treatment) resulted in only a 60 per cent decrease in stand water use.

The effect of thinning on stand water use was able to be modelled successfully using a simple canopy size modifier with the Penman-Monteith equation.

10.2.5 Photosynthesis and nutrient levels (chapter 8)

Photosynthetic rates, measured at constant illumination, increased throughout the crown following thinning. The greatest increases were observed in the lower and middle crown zones. Photosynthetic rate was positively related to foliar nitrogen concentration. Thinning increased foliar nitrogen and phosphorus concentrations on a leaf area basis because of a significant decrease in specific leaf area after thinning (*ie.* thicker leaves). Changes in photosynthetic rates, specific leaf area and foliar nutrient distributions with thinning were well correlated with changes in the levels of incident light throughout the individual tree crown.

10.2.6 Significance of physiological changes (chapter 9)

A modelling analysis was undertaken to examine the impact that physiological changes after thinning have on stem growth. A light-use efficiency approach was taken. Thinning increases crown light interception, improves photosynthetic light-use efficiency and alters patterns of biomass partitioning between tree components. The changes in crown dynamics after thinning, specifically the changes in light interception and light-use efficiency were the parameters that had

the greatest impact on stem growth.

10.3 Management implications

The implications of the findings are discussed in the context of the following four questions that pertain to the management of eucalypt sawlog plantations;

(1) at what age should thinning be done?

(2) what is the ideal residual stand density?

(3) does variation in site quality affect questions (1) and (2)?

(4) how should thinning and pruning operations be scheduled in a sawlog regime for eucalypt plantations?

10.3.1 Timing of thinning

The early years (0-4 years) of growth of an *E. nitens* plantation established at a density of 1100 trees ha^{-1} are characterised by high tree growth rates. At the age of canopy closure (typically age 3 to 4 years on good quality sites, Smethurst 1998), the site can be considered as fully occupied by the stand and L tends to stabilise (eg. Hingston et al. 1994) or gradually decline (Jarvis and Leverenz 1983). Beyond this point, while growth remains high on a stand-basis, the rate of individual tree growth slows due to competition for light, water and nutrients from neighbouring trees. From a biological viewpoint, thinning close to the age that full canopy closure is reached (when the crowns of trees in adjacent rows touch) is ideal as the rapid stem growth at the individual tree level is maintained. After canopy closure, the vertical distribution of leaf area in *E. nitens* plantations can change from a 'normal' distribution to a skewed distribution (Pinkard and Beadle

1998b) as canopy lift associated with leaf and branch senescence occurs under the low light conditions. Timing thinning to coincide with the age of canopy closure maintains the light levels required for activity throughout the crown (eg. Figure 10.1).

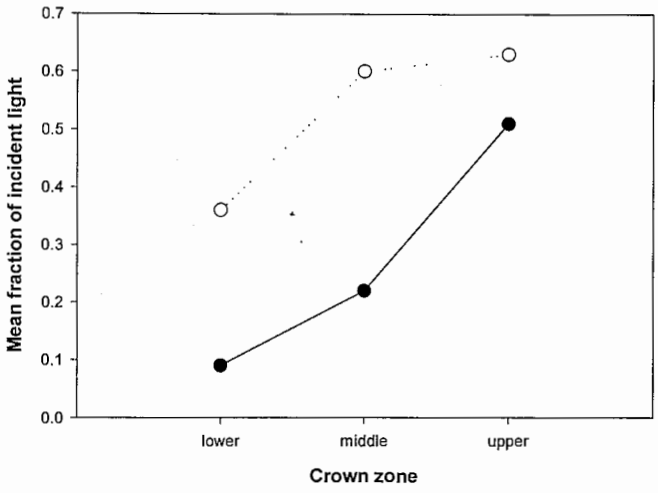


Figure 10.1 Changes in the levels of incident light with crown depth after thinning at Creekton. (●—● unthinned stand, O····O stand thinned to 250 tree ha^{-1}).

From an economic point of view, an early thinning may not be ideal as the burden of carrying establishment costs until the end of the rotation can be relieved by a commercial thinning when trees reach the appropriate size (Gerrand et al. 1993; Candy and Gerrand 1997). So what is the potential loss in individual tree growth incurred by delaying thinning in *E. nitens* plantations until a commercial thinning can be done? Nine years of post-thinning growth data from the Goulds Country thinning trial enables this question to be examined.

Thinning treatment was imposed at Goulds Country at age six years (full canopy

closure had not yet occurred on this moderate quality site). At age 12 years, the top 200 trees ha^{-1} in the unthinned stand achieved the average stem diameter of 24.5 cm. The average diameter of trees thinned to 200 trees ha^{-1} was 30.5 cm. This 24 per cent gain in stem diameter by thinning early is equivalent to a 55 per cent gain in mean tree basal area (Figure 10.2). The early thinning will result in either larger trees at the end of a specified rotation length, or allow a shorter rotation to achieve a specified stem size. This needs to be considered in any financial analysis of sawlog regimes for *E. nitens* plantations.

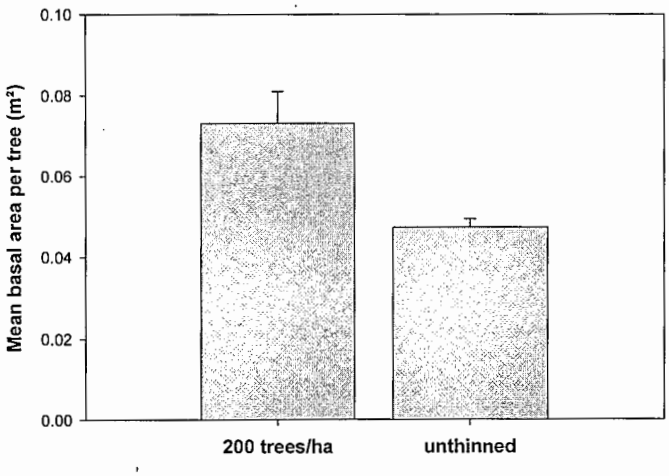


Figure 10.2 Mean basal area per tree of the 200 trees ha^{-1} treatment and the top 200 trees ha^{-1} in the unthinned treatment at age 12 years, Goulds Country thinning trial. Error bars show one standard deviation.

This study has demonstrated that a thinning response in the form of greater stem growth can still be achieved when thinning is delayed beyond canopy closure. In the stands that were studied, *E. nitens* was able to meet the extra demand for water from the more exposed crowns by increasing the hydraulic conductivity of the

sapwood. In addition, trees were able to adjust leaf morphology in response to the improvement in the light environment to increase the photosynthetic activity. These physiological changes can be considered in the light of findings that thinning eucalypt plantations after appreciable crown lift and lowered live crown ratio does not improve growth rates (eg. Gerrand et al. 1997a). Increased hydraulic resistance with tree age and height may lower stomatal conductance and hence carbon assimilation (Yoder et al. 1994; Ryan et al. 1997). However, for the ages at which thinning is proposed for *E. nitens* plantations (between 8 to 12 years), the decrease in hydraulic conductivity is expected to be minimal, and unlikely to be a major determinant of thinning response. The effect of leaf area per tree, and how this changes with stand development to age 12 years is likely to have the greatest impact on the magnitude of thinning response. The stage of the rotation at which *E. nitens* will not respond to thinning may be linked to the extent of 'crown lift' and the resulting ratio of crown length (as a measure of crown size) to tree height (as a measure of respiring sapwood surface area). As this ratio decreases, the extra photosynthate gained from thinning may be offset by the increases in respiration caused by greater temperatures (Jarvis and Leverenz 1983; Criddle et al. 1996).

10.3.2 Intensity of thinning

The improvement in stem growth response to thinning will increase with increasing thinning intensity. For most *E. nitens* plantations in Tasmania, the main factor behind this increased growth is the improvement in the light environment for each tree crown. The amount of light absorbed per tree will increase in a non-linear fashion with decreasing stand density (Bartelink 1998a). Figure 10.3 shows, in a thinning study of a mixed species *P. radiata – Acacia melanoxylon* R. Br.

plantation, that the fraction of light reaching 1.3 m height did not increase until more than 50 per cent of the *P. radiata* trees were removed (Medhurst, unpublished data). While differences exist between the crown architecture of *P. radiata* and *E. nitens*, the non-linear nature of the relationship is expected to also apply for *E. nitens* plantations. This indicates that, for a closed canopy stand of *E. nitens*, removing more than 50 per cent of trees is required to improve the light environment for the crowns of the retained trees.

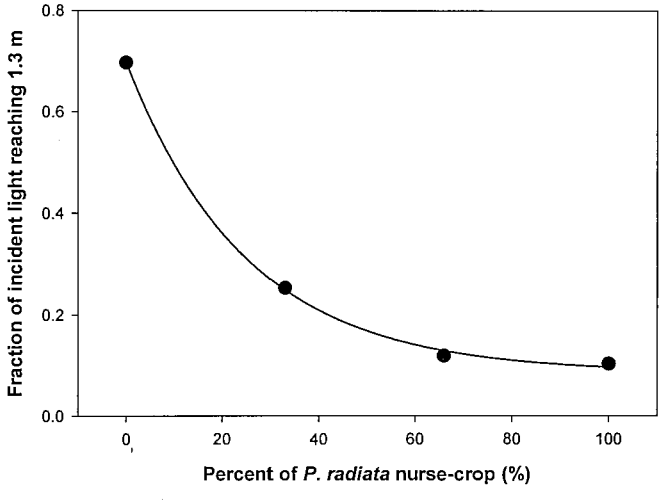


Figure 10.3 Effect of decreasing nurse-crop stand density on the degree of intercepted light in a *P. radiata* – *A. melanoxylon* plantation (Medhurst, unpublished data).

The amount of light intercepted by canopies also depends on their architecture (Cannell 1989b). Thinning to a stand density that allows a large proportion of daily radiation to penetrate to the lower crowns of retained trees will alter the crown architecture of the retained trees. Most notably, the vertical distribution of

leaf area will change as branches in the lower and middle sections of the crown increase in size. That is, the crowns will develop to maximise light interception. The potential impacts of inter-tree competition on the maximisation of light interception by individual trees should be minimised (Figure 6.5). From this finding it is proposed that the ideal residual stand density after thinning is that which will lead to maximum L of the site being reached towards the end of the rotation. This stand density would allow maximum light interception by individual crowns without unnecessary loss of site occupancy over the course of the rotation. Our understanding of L development after thinning is limited and is an area for further research. The change in L at the Goulds Country thinning trial, six years after thinning (Figure 6.7a) and approximately eight years from final harvest suggests that a stand density between 200 and 300 trees ha^{-1} may attain maximum L at this site. The reduced rate of stand basal area growth of the 100 trees ha^{-1} treatment at this trial indicates that this stand is considerably below full site occupancy and structural limitations to maximum crown expansion are likely to preclude this stand from reaching maximum L.

10.3.3 Site quality considerations

It is difficult to draw definitive conclusions on the effects of site quality on timing and intensity of thinning due to the limited number of sites used in this study. However, an understanding of how site quality affects canopy size and dynamics enables some tentative conclusions to be drawn. The dynamics and size of a forest canopy are strongly controlled by the availability of soil water and nutrients (Burton et al. 1991; White 1996; Jose and Gillespie 1997; Battaglia et al. 1998). Consequently, for *E. nitens* plantations on sites of low quality, the maximum L that can be achieved will be lower than that on a high quality site and the rate of L

development will be slower (Cromer et al. 1993; White 1996). Thinning treatment alone does not alter the potential maximum L achievable at a given site, but rather re-distributes the leaf area onto fewer trees. On a low quality site, the site limitations to L development may prevent canopy re-closure if the thinning is of a sufficient intensity. For the same thinning intensity, the rate and extent of canopy re-closure on a high quality will be greater. If the concept of thinning to reach maximum site L at the end of the rotation is adopted, the residual stand density on low quality sites can be higher than that of high quality sites. The same residual stand densities following thinning on low as high productivity sites would still produce a growth response in retained trees. However full site occupancy may not be regained. Essentially, thinning intensity needs to increase with increasing site quality to meet the criteria of reaching maximum site L at the end of the rotation. However by adopting such a criteria, smaller individual tree sizes must be accepted on lower quality sites.

When compared with less productive plantations, the higher L at canopy closure of highly productive eucalypt plantations is usually expressed by longer crown lengths (eg. Cromer et al. 1993; Gerrand et al. 1997a). Light is attenuated through a closed canopy in an exponential manner. Hence for an individual tree crown, the change in light environment after thinning for the lower crown will increase with increasing crown length. Due to this difference in architecture, the capacity for trees to respond to thinning after canopy closure increases with site quality. Thus, to maintain adequate growth of final crop trees, plantations on less productive sites should be thinned at, or soon after, canopy closure. Delaying thinning on high quality sites, up to a point, will not preclude a growth response.

10.3.4 Scheduling thinning and pruning

The different responses of *E. nitens* to thinning and selective pruning means that the scheduling of these operations can have a large bearing on final tree size and wood quality. The increased light interception and improved photosynthetic capacity of the lower and middle crown drive the growth response of *E. nitens* to thinning. Pruning of up to 50 per cent of green crown length in high quality *E. nitens* plantations is possible without loss of growth as light interception of the crown in a closed canopy stand is not affected by loss of this lower section (Pinkard et al. 1999). Consequently, closely scheduled thinning and pruning operations will reduce the potential response to thinning because of the loss of the lower crown. Conversely, thinning at time of pruning may minimise the negative growth impact of more intensive pruning, and reduce the number of pruning lifts required to meet pruned log specifications. Thinning at time of pruning to reduce competition for light has been suggested as a means of minimising this decline in growth rate (Sutton and Crowe 1975; Karani 1978). In a closed canopy *E. nitens* plantation, pruning 70 per cent of green crown length resulted in loss of dominance and growth (Pinkard and Beadle 1998a). The improved light conditions and photosynthetic capacity after thinning a closed *E. nitens* plantation are confined largely to the lower and middle sections of the crown. Therefore, thinning may offset the growth loss after pruning less than two-thirds of green crown length. However, the negative impact of pruning more than two-thirds of green crown length is unlikely to be arrested by simultaneous thinning. In addition, as thinning will alter the vertical distribution of leaf area in the crown, subsequent pruning treatment after thinning will remove a higher proportion of total crown leaf area for a given crown length.

The current sawlog prescription for *E. nitens* plantations of low productivity schedules a first-lift pruning only (to 2.5 m) followed by an early non-commercial thinning (at age 6 or 7 years) to final stand density (Forestry Tasmania 1999). In these plantations, minimal pruning followed by early thinning will allow the lower and middle sections of the crown of retained trees to develop and respond to thinning treatment. In highly productive plantations, the current prescription delays thinning until a commercial thinning can be carried out (between age 8 to 12 years) and prunes to 6.4 m in three lifts, each removing no more than 50 per cent of green crown length (Forestry Tasmania 1999). This approach will maintain the growth rate of the pruned trees relative to their unpruned neighbours. Loss of leaf area from further crown lift after the final pruning will reduce the potential growth response to thinning. Ideally then, delayed thinning is scheduled when the crown base of unpruned trees reaches 6.4 m.

References

ABARE 1998. Australian Forest Products Statistics – June quarter 1998, Australian Bureau of Agricultural and Resource Economics,

Acock, M.C., Daughtry, C.S.T., Beinhart, G., Hirschmann, E. and Acock, B. 1994. Estimating leaf mass from light interception measurements on isolated plants of *Erythroxylum* species. *Agronomy Journal* 86:570–574.

Albrektson, A. 1984. Sapwood basal area and needle mass of Scots pine (*Pinus sylvestris* L.) trees in central Sweden. *Forestry* 57:35–43.

Aussenac, G. and Granier, A. 1988. Effects of thinning on water stress and growth in Douglas–fir. *Canadian Journal of Forest Research* 18:100–105.

Axelsson, E. and Axelsson, B. 1986. Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. *Tree Physiology* 2:189—204.

Bailey, R.L. and Dell, T.R. 1973. Quantifying diameter distributions with the Weibull function. *Forest Science* 19:97–104.

Barrett, D.J., Hatton, T.J., Ash, J.E. and Ball, M.C. 1995. Evaluation of the heat pulse velocity technique for measurement of sap flow in rainforest and eucalypt forest species of south–eastern Australia. *Plant, Cell and Environment* 18:463–469.

Bartelink, H.H. 1996. Allometric relationships on biomass and needle area of Douglas–fir. *Forest Ecology and Management* 86:193–203.

Bartelink, H.H. 1997. Allometric relationships for biomass and leaf area of beech (*Fagus sylvatica* L). *Annales des Sciences Forestieres* 54:39–50.

Bartelink, H.H. 1998a. Radiation interception by forest trees: a simulation study on effects of stand density and foliage clustering on absorption and transmission. *Ecological Modelling* 105:213–225.

Bartelink, H.H. 1998b. A model of dry matter partitioning in trees. *Tree Physiology* 18:91–101.

Battaglia, M., Beadle, C. and Loughhead, S. 1996. Photosynthetic temperature responses of *Eucalyptus globulus* and *Eucalyptus nitens*. *Tree Physiology* 16:81–89.

Battaglia, M. and Sands, P. 1997. Modelling site productivity of *Eucalyptus globulus* in response to climatic and site factors. *Australian Journal of Plant Physiology* 24:831–850.

Battaglia, M., Cherry, M.L., Beadle, C.L., Sands, P.J. and Hingston, A. 1998. Prediction of leaf area index in eucalypt plantations: effects of water stress and temperature. *Tree Physiology* 18:521–528.

Battaglia, M. and Sands, P.J. 1998. Process–based forest productivity models and their application in forest management. *Forest Ecology and Management* 102:13–32.

Beadle, C.L. and Mummery, D.C. 1989. Stand growth and development of leaf area index in young plantations of *Eucalyptus nitens* at 2 x 2 m spacings. *New Zealand Forest Research Institute Bulletin* 151:254–258.

Beadle, C.L. and Inions, G. 1990. Limits to growth of eucalypts and their biology of production. *In* Prospects for Australian forest plantations. *Eds*. Dargavel, J. and Semple, N., Centre for Resource and Environmental Studies, A.N.U., Canberra, pp 183–193.

Beadle, C.L. and Turnbull, C.R.A. 1992. Comparative growth rates of *Eucalyptus* in native forest and in plantation monoculture. *In* Growth and water use of forest plantations. *Eds*. Calder, I.R., Hall, R.L. and Adlard, P.G., John Wiley & Sons, Chichester, pp 318–331.

Beadle, C.L. 1993. Growth analysis. *In* Photosynthesis and production in a changing environment – a field and laboratory manual. *Eds*. Hall, D.O., Scurlock, J.M.O., Bolhàr–Nordenkampf, H.R., Leegood, R.C. and Long, S.P., Chapman & Hall, London, pp 36–46.

Beadle, C.L., Honeysett, J.L., Turnbull, C.R.A. and White, D.A. 1995. Site limits to achieving genetic potential. *In* Eucalypt plantations: improving fibre yield and quality *Eds*. Potts, B.M., Borralho, N.M.G., Reid, J.B., Cromer, R.N., Tibbits, W.N. and Raymond, C.A. Hobart, Australia, IUFRO and Cooperative Research Centre for Temperate Hardwood Forestry, pp 325–330.

Beadle, C.L. 1997. Dynamics of leaf and canopy development. *In* Management of soil, nutrients and water in tropical plantation forests. *Eds*. Nambiar, E.K.S. and Brown, A.G., Australian Centre for International Agricultural Research (ACIAR), Canberra, Australia, pp 169–212.

Beets, P.N. and Pollock, D.S. 1987. Accumulation and partitioning of dry matter in *Pinus radiata* as related to stand age and thinning. *New Zealand Journal of Forestry Science* 17:246–271.

Bennett, L.T., Weston, C.J. and Attiwill, P.M. 1997. Biomass, nutrient content and growth response to fertilsers of six–year–old *Eucalyptus globulus* plantations at three contrasting sites in Gippsland, Victoria. *Australian Journal of Botany* 45:103–121.

Benyon, R.G., Marcar, N.E., Crawford, D.F. and Nicholson, A.T. 1999. Growth and water use of *Eucalyptus camaldulensis* and *E. occidentalis* on a saline discharge site near Wellington, NSW, Australia. *Agricultural Water Management* 39:229–244.

Bernardo, A.L., Reis, M.G.F., Reis, G.G., Harrison, R.B. and Firme, D.J. 1998. Effect of spacing on growth and biomass distribution in *Eucalyptus camaldulensis, E. pellita* and *E. urophylla* plantations in southeastern Brazil. *Forest Ecology and Management* 104:1–13.

Berninger, F. and Nikinmaa, E. 1997. Implications of varying pipe model relationships on Scots Pine growth in different climates. *Functional Ecology* 11:146–156.

Binkley, D. 1984. Douglas-fir stem growth per unit of leaf area increased by interplanted sitka alder and red alder. *Forest Science* 30:259—263.

Birk, E.M. and Turner, J. 1992. Response of flooded gum (*E. grandis*) to intensive cultural treatments: biomass and nutrient content of eucalypt plantations and native forests. *Forest Ecology and Management* 47:1–28.

Blanche, C.A. and Hodges, J.D. 1985. A leaf area – sapwood area ratio developed to rate loblolly pine vigor. *Canadian Journal of Forest Research* 15:1181–1184.

Boardman, R., Lambert, M.J., Webb, M. and Cromer, R.N. 1997. Forest Plantations. *In* Plant Analysis: An Interpretation Manual. *Eds*. Reuter, D.J. and Robinson, J.B., CSIRO Publishing, Collingwood, Victoria, pp 503—566.

Boland, D.J., Brooker, M.I.H., Chippendale, G.M., Hall, N., Hyland, B.P.M., Johnston, R.D., Kleinig, D.A. and Turner, J.D. 1984. Forest trees of Australia. 4th ed. Thomas Nelson Australia and CSIRO, Melbourne.

Bonny, L. 1991. Growth of a *Eucalyptus grandis* plantation following intensive silvicultural treatments applied in the first six years, Forestry Commission of New South Wales, Research Paper 12.

Booker, R.E. and Kininmonth, J.A. 1978. Variation in longitudinal permeability of green radiata pine wood. *New Zealand Journal of Forestry Science* 8:295—308.

Borghetti, M., Cinnirella, S., Magnani, F. and Saracino, A. 1998. Impact of long–term drought on xylem embolism and growth in *Pinus halepensis* Mill. *Trees* 12:187–195.

Bréda, N., Granier, A. and Aussenac, G. 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiology* 15:295–306.

Brix, H. 1981. Effects of thinning and nitrogen fertilization on branch and foliage production in Douglas–fir. *Canadian Journal of Forest Research* 11:502–511.

Brix, H. and Mitchell, A.K. 1983. Thinning and nitrogen fertilization effects on sapwood development and relationships of foliage quantity to sapwood area and basal area in Douglas–fir. *Canadian Journal of Forest Research* 13:384–389.

Brown, G. 1997. Growth responses to thinning in eucalypt regrowth forests. *Tasforests* 9:105–122.

Burton, A.J., Pregitzer, K.S. and Reed, D.D. 1991. Leaf area and foliar biomass relationships in northern hardwood forests located along an 800 km acid deposit gradient. *Forest Science* 37:1041—1059.

Calder, I.R. 1992. Water use of eucalypts — a review. *In* Growth and Water Use of

Forest Plantations. *Eds*. Calder, I.R., Hall, R.L. and Adlard, P.G., John Wiley & Sons, pp 167—179.

Calder, I.R., Swaminath, M.H., Kariyappa, G.S., Srinivasalu, N.V., Srinivasa Murthy, K.V. and Mumtaz, J. 1992. Measurements of transpiration from *Eucalyptus* plantations, India, using deuterium tracing. *In* Growth and Water Use of Forest Plantations. *Eds*. Calder, I.R., Hall, R.L. and Adlard, P.G., John Wiley & Sons, West Sussex, England, pp 196—215.

Candy, S.G. 1997. Growth and yield models for *Eucalyptus nitens* plantations in Tasmania and New Zealand. *Tasforests* 9:167–198.

Candy, S.G. and Gerrand, A.M. 1997. Comparison of financial returns from sawlog regimes for *Eucalyptus nitens* plantations in Tasmania. *Tasforests* 9:35–50.

Cannell, M.G.R. 1989a. Physiological basis of wood production: a review. *Scandinavian Journal of Forest Research* 4:459–490.

Cannell, M.G.R. 1989b. Light interception, light use efficiency and assimilate partitioning in poplar and willow stands. *In* Biomass production by fast growing trees. *Eds*. Pereira, J.S. and Landsberg, J.J., Kluwer Academic Publishers, pp 1–12.

Cannell, M.G.R. and Dewar, R.C. 1994. Carbon allocation in trees: a review of concepts for modelling. *Advances in Ecological Research* 25:59–104.

Causton, D.R. 1985. Biometrical, structural and physiological relationships among tree parts. *In* Attributes of trees as crop plants. *Eds*. Cannell, M.G.R. and Jackson, J.E., Institute of Terrestrial Ecology, Great Britain, pp 137–159.

Cherry, M.L., Hingston, A., Battaglia, M. and Beadle, C.L. 1998. Calibrating the LI–COR LAI–2000 for estimating leaf area index in eucalypt plantations.

Tasforests 10:75–82.

Colin, F., Houllier, F., Joannes, H. and Haddaoui, A. 1993. A model of the vertical distribution of diameters, angles and numbers of branches of three *Picea abies* provenances. *Silvae Genetica* 42:206–222.

Courbaud, B. 2000. Comparing light interception with stand basal area for predicting tree growth. *Tree Physiology* 20:407—414.

Coyea, M.R. and Margolis, H.A. 1992. Factors affecting the relationship between sapwood area and leaf area of balsam fir. *Canadian Journal of Forest Research* 22:1684–1693.

Cregg, B.M., Hennessey, T.C. and Dougherty, P.M. 1990. Water relations of loblolly pine trees in southeastern Oklahoma following precommercial thinning. *Canadian Journal of Forest Research* 20:1508–1513.

Cremer, K.W., Borough, C.J., McKinnell, F.H. and Carter, P.R. 1982. Effects of stocking and thinning on wind damage in plantations. *New Zealand Journal of Forestry Science* 12:244–268.

Criddle, R.S., Anekonda, T.S., Sachs, R.M., Breindenbach, R.W. and Hansen, L.D. 1996. Selection for biomass production based on respiration parameters in eucalypts: acclimation of growth and respiration to changing growth temperature. *Canadian Journal of Forest Research* 26:1569–1576.

Cromer, R.N. and Jarvis, P.G. 1990. Growth and biomass partitioning in *Eucalyptus grandis* seedlings in response to nitrogen supply. *Australian Journal of Plant Physiology* 17:503–515.

Cromer, R.N., Cameron, D.M., Rance, S.J., Ryan, P.A. and Brown, M. 1993. Response to nutrients in *Eucalyptus grandis*. 1. Biomass accumulation. *Forest*

Ecology and Management 62:211—230.

David, T.S., Ferreira, M.I., David, J.S. and Pereira, J.S. 1997. Transpiration from a mature *Eucalyptus globulus* plantation in Portugal during a spring–summer period of progressively higher water deficit. *Oecologia* 110:153–159.

de Pury, D.G.G. and Farquhar, G.D. 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big–leaf models. *Plant, Cell and Environment* 20:537–557.

Deadman, H. and Hay, A.E. 1987. Eucalypts – selecting high quality crop trees. *In* What's New in Forest Research no. 155; Forest Research Institute, Rotorua, New Zealand, 4 pp.

Dean, T.J. and Long, J.N. 1986. Variation in sapwood area–leaf area relations within two stands of lodgepole pine. *Forest Science* 32:749–758.

DeJong, T.M., Day, K.R. and Johnson, R.S. 1989. Partitioning of leaf nitrogen with respect to within canopy light exposure and nitrogen availability in peach (*Prunus persica*). *Trees* 3:89—95.

Donner, B.L. and Running, S.W. 1986. Water stress response after thinning *Pinus contorta* stands in Montana. *Forest Science* 32:614–625.

Dunn, G.M. and Connor, D.J. 1993. An analysis of sap flow in mountain ash (*Eucalyptus regnans*) forests of different age. *Tree Physiology* 13:321–336.

Dye, P.J., Olbrich, B.W. and Poulter, A.G. 1991. The influence of growth rings in *Pinus patula* on heat pulse velocity and sap flow measurements. *Journal of Experimental Botany* 42:867—870.

Dye, P.J. and Olbrich, B.W. 1993. Estimating transpiration from 6–year–old

Eucalyptus grandis trees: development of a canopy conductance model and comparison with independent sap flux measurements. *Plant, Cell and Environment* 16:45–53.

Edwards, W.R.N. and Jarvis, P.G. 1982. Interactions between water content, potential and permeability in stems of conifers. *Plant, Cell and Environment* 5:271–277.

Edwards, W.R.N. and Booker, R.E. 1984. Radial variation in the axial conductivity of *Populus* and its significance in heat pulse velocity measurement. *Journal of Experimental Botany* 35:551—561.

Edwards, W.R.N., Becker, P. and Cermák, J. 1996. A unified nomenclature for sap flow measurements. *Tree Physiology* 17:65–67.

Espinosa-Bancalari, M.A., Perry, D.A. and Marshall, J.D. 1987. Leaf area – sapwood area relationships in adjacent young Douglas–fir stands with different early growth rates. *Canadian Journal of Forest Research* 17:174–180.

Evans, J.R. 1989. Partitioning of nitrogen between and within leaves grown under difference irradiances. *Australian Journal of Plant Physiology* 16:533—548.

Farmer, B. and Smith, P. 1997. Plantation establishment under the Intensive Forest Management Program 1991–96. *Tasforests* 9:1–6.

Field, C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* 56:341—347.

Florence, R.G., Turner, B.J., Byron, R.N., Groves, K.W. and Davey, S.M. 1990. Problems in formulating an Australian plantation policy. *In* Prospects for Australian forest plantations. *Eds*. Dargavel, J. and Semple, N., Centre for Resource and Environmental Studies, Australian National University, Canberra, pp 25–37.

Ford, E.D. 1985. Branching, crown structure and the control of timber production. *In* Attributes of trees as crop plants. *Eds*. Cannell, M.G.R. and Jackson, J.E., Institute of Terrestrial Ecology, Great Britain, pp 228–252.

Forestry Tasmania 1999. Prescriptions for pruning and thinning eucalypts in plantations for clearwood production. Division of Forest Research and Development, Hobart, 26 pp.

Fownes, J.H. and Harrington, R.A. 1990. Modelling growth and optimal rotations of tropical multipurpose trees using unit leaf rate and leaf area index. *Journal of Applied Ecology* 27:886–896.

Fownes, J.H. and Harrington, R.A. 1992. Allometry of woody biomass and leaf area in five tropical multipurpose trees. *Journal of Tropical Forest Science* 4:317–330.

Fry, G. 1983. Eucalypts in New Zealand: a position report. *New Zealand Journal of Forestry* 28:394–411.

Gary, H.L. 1974. Canopy weight distribution affects windspeed and temperature in a lodgepole pine forest. *Forest Science* 20:369–371.

Gary, H.L. 1978. The vertical distribution of needles and branchwood in thinned and unthinned 80–year–old lodgepole pine. *Northwest Science* 52:303–309.

Gerrand, A., Prydon, R. and Fenn, G. 1993. A financial evaluation of eucalypt plantations in Tasmania. *Tasforests* 5:77–97.

Gerrand, A.M., Medhurst, J.L. and Neilsen, W.A. 1997a. Research results for thinning and pruning eucalypt plantations for sawlog production in Tasmania, Forests and Forest Industry Council of Tasmania and Forestry Tasmania, 209 pp.

Gerrand, A.M., Neilsen, W.A. and Medhurst, J.L. 1997b. Thinning and pruning eucalypt plantations for sawlog production in Tasmania. *Tasforests* 9:15–34.

Gillespie, A.R., Allen, H.L. and Vose, J.M. 1994. Amount and vertical distribution of foliage of young loblolly pine trees as affected by canopy position and silvicultural treatment. *Canadian Journal of Forest Research* 24:1337–1344.

Ginn, S.E., Seiler, J.R., Cazell, B.H. and Kreh, R.E. 1991. Physiological and growth responses of eight–year–old loblolly pine stands to thinning. *Forest Science* 37:1030–1040.

Givnish, T.J. 1988. Adaption to sun and shade: a whole-plant perspective. *Australian Journal of Plant Physiology* 15:63—92.

Goodwin, A. 1990. Thinning response in eucalypt regrowth. *Tasforests* 2:27–35.

Gratani, L. 1997. Canopy structure, vertical radiation profile and photosynthetic function in a *Quercus ilex* evergreen forest. *Photosynthetica* 33:139–149.

Gravatt, D.A., Chambers, J.L. and Barnett, J.P. 1997. Temporal and spatial patterns of net photosynthesis in 12–year–old loblolly pine five growing seasons after thinning. *Forest Ecology and Management* 97:73–83.

Green, S.R. 1993. Radiation balance, transpiration and photosynthesis of an isolated tree. *Agricultural and Forest Meteorology* 64:201—221.

Grier, C.C. and Waring, R.H. 1974. Conifer foliage mass related to sapwood area. *Forest Science* 20:205–206.

Hacke, U.J. and Sauter, J.J. 1996. Xylem disfunction during winter and recovery of hydraulic conductivity in diffuse–porous and ring–porous trees. *Oecologia* 105:435–439.

Hasenauer, H., Burkhart, H.E. and Amateis, R.L. 1997. Basal area development in thinned and unthinned loblolly pine plantations. *Canadian Journal of Forest Research* 27:265–271.

Hatton, T., Reece, P., Taylor, P. and McEwan, K. 1998. Does leaf water efficiency vary among eucalypts in water–limited environments? *Tree Physiology* 18:529–536.

Hatton, T.J., Catchpole, E.A. and Vertessy, R.A. 1990. Integration of sapflow velocity to estimate plant water use. *Tree Physiology* 6:201–209.

Hatton, T.J., Moore, S.J. and Reece, P.H. 1995. Estimating stand transpiration in a *Eucalyptus populnea* woodland with the heat pulse method: measurement errors and sampling strategies. *Tree Physiology* 15:219–227.

Hingston, F.J., Galbraith, J.H. and Dimmock, G.M. 1994. Evaluating the effect of soils and climate on productivity of *Eucalyptus globulus* plantations on contrasting sites in south west of Western Australia, Rural Industries Research and Development Corporation, Final Report, No. CSF-41A, 52 pp.

Hogg, E.H. and Hurdle, P.A. 1997. Sap flow in trembling aspen: implications for stomatal responses to vapour pressure deficit. *Tree Physiology* 17:501–509.

Hollinger, D.Y. 1989. Canopy organization and foliage photosynthetic capacity in a broad–leaved evergreen montane forest. *Functional Ecology* 3:53–62.

Honeysett, J.L., Beadle, C.L. and Turnbull, C.R.A. 1992. Evapotranspiration and growth of two contrasting species of eucalypts under non–limiting and limiting water availability. *Forest Ecology and Management* 50:203–216.

Honeysett, J.L., White, D.A., Worledge, D. and Beadle, C.L. 1996. Growth and water use of *Eucalyptus globulus* and *E. nitens* in irrigated and rainfed plantations.

Australian Forestry 59:64–73.

Horne, R. and Robinson, G. 1990. Growth response following variable espacement of 28–year–old alpine ash regeneration in New South Wales. *Australian Forestry* 53:280–289.

Hunt, M.A. and Beadle, C.L. 1998. Whole–tree transpiration and water–use partitioning between *Eucalyptus nitens* and *Acacia dealbata* weeds in a short–rotation plantation in northeastern Tasmania. *Tree Physiology* 18:557–563.

Hunt, M.A. 1999. Competition between plantation *Eucalyptus nitens* (Deane and Maiden) Maiden and naturally regenerating *Acacia dealbata* Link. PhD thesis, University of Tasmania, 161 pp.

Hunt, M.A., Unwin, G.L. and Beadle, C.L. 1999. Effects of naturally regenerated *Acacia dealbata* on the productivity of a *Eucalyptus nitens* plantation in Tasmania, Australia. *Forest Ecology and Management* 117:75–85.

Hutchinson, B.A., Matt, D.R. and McMillen, R.T. 1986. The architecture of a deciduous forest canopy in eastern Tennessee. *Journal of Ecology* 74:635–646.

Jarvis, P.G. 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London* 273:593–610.

Jarvis, P.G. and Leverenz, J. 1983. Productivity of temperate, deciduous and evergreen forests. *In* Encyclopedia of plant physiology. New Series, Volume 12D. *Eds*. Lange, O.L., Nobel, P.S., Osmond, C.B. and Ziegler, H., Springer–Verlag, Berlin, pp 233–280.

Jarvis, P.G. and McNaughton, K.G. 1986. Stomatal control of transpiration: scaling

up from leaf to region. *Advances in Ecological Research* 15:1—49.

Jose, S. and Gillespie, A.R. 1997. Leaf area–productivity relationships among mixed–species hardwood forest communities of the central hardwood region. *Forest Science* 43:56–64.

Judd, T.S., Attiwill, P.M. and Adams, M.A. 1991. Foliar diagnosis of plantations of *Eucalyptus globulus* and *E. nitens* in southeastern Australia. *In* Productivity in Perspective, Proceedings of the 3rd Australian Forest Soils and Nutrition Conference *Ed.* Ryan, P.J. Melbourne, Victoria, pp 162—163.

Karani, P.K. 1978. Pruning and thinning in a *Pinus patula* stand at Lendu plantation, Uganda. *Commonwealth Forestry Review* 57:269—278.

Kaufmann, M.R. and Troendle, C.A. 1981. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. *Forest Science* 27:477–482.

Kazda, M., Salzer, J. and Reiter, I. 2000. Photosynthetic capacity in relation to nitrogen in the canopy of a *Quercus robur*, *Fraxinus angustifolia* and *Tilia cordata* flood plain forest. *Tree Physiology* 20:1029—1037.

Keane, M.G. and Weetman, G.F. 1987. Leaf area – sapwood cross–sectional area relationship in repressed stands of lodgepole pine. *Canadian Journal of Forest Research* 17:205–209.

Kellomäki, S., Oker–Blom, P. and Kuuluvainen, T. 1985. The effect of crown and canopy strucure on light interception and distribution in a tree stand. *In* Crop physiology of forest trees. *Eds.* Tigerstedt, P.M.A., Puttonen, P. and Koski, V., University of Helsinki, Dept. of Plant Breeding, Finland, Helsinki, pp 107–115.

Kellomäki, S. and Wang, K.Y. 1997. Effects of long–term CO_2 and temperature elevation on crown nitrogen distribution and daily photosynthetic performance of Scots pine. *Forest Ecology and Management* 99:309–326.

Kerr, G. 1996. The effect of heavy or 'free growth' thinning on oak (*Quercus petraea* and *Q. robur*). *Forestry* 69:303–317.

King, D.A. 1998. Relationship between crown architecture and branch orientation in rain forest trees. *Annals of Botany* 82:1–7.

Kirschbaum, M. and Tompkins, D. 1990. Photosynthetic responses to phosphorus nutrition in *Eucalyptus grandis* seedlings. *Australian Journal of Plant Physiology* 17:527—535.

Koistinen, E. 1985. Effect of thinnings in planted Norway spruce stands. *In* Crop physiology of forest trees. *Eds*. Tigerstedt, P.M.A., Puttonen, P. and Koski, V., University of Helsinki, Dept. of Plant Breeding, Helsinki, pp 307–313.

Korzukhin, M.D. and Ter-Mikaelian, M.T. 1995. An individual tree–based model of competition for light. *Ecological Modelling* 79:221–229.

Landsberg, J.J. and McMurtie, R. 1985. Models based on physiology as tools for research and forest management. *In* Research for forest management. *Eds*. Landsberg, J.J. and Parsons, W., CSIRO, Melbourne, pp 214–228.

Landsberg, J.J. and Hingston, F.J. 1996. Evaluating a simple radiation/dry matter conversion model using data from *Eucalyptus globulus* plantations in Western Australia. *Tree Physiology* 16:801–808.

Landsberg, J.J. and Waring, R.H. 1997. A generalized model of forest productivity using simplified concepts of radiation–use efficiency, carbon balance and partitioning. *Forest Ecology and Management* 95:209–228.

Lanner, R.M. 1985. On the insensitivity of height growth to spacing. *Forest Ecology and Management* 13:143–148.

Larsen, D.R. and Kernshaw Jr., J.A. 1996. Influence of canopy structure assumptions on predictions from Beer's law. A comparison of deterministic and stochastic simulations. *Agricultural and Forest Meteorology* 81:61–77.

Lavigne, M.B. 1987. Differences in stem respiration responses to temperature between balsam fir trees in thinned and unthinned stands. *Tree Physiology* 3:225–233.

Lavigne, M.B. 1988. Stem growth and respiration of young balsam fir trees in thinned and unthinned stands. *Canadian Journal of Forest Research* 18:483—489.

Le Roux, X., Sinoquet, H. and Vandame, M. 1999. Spatial distribution of leaf dry weight per area and leaf nitrogen concentration in relation to local radiation regime within an isolated tree crown. *Tree Physiology* 19:181—188.

Leuning, R., Cromer, R.N. and Rance, S. 1991a. Spatial distributions of foliar nitrogen and phosphorus in crowns of *Eucalyptus grandis*. *Oecologia* 88:504–510.

Leuning, R., Wang, Y.P. and Cromer, R.N. 1991b. Model simulations of spatial distributions and daily totals of photosynthesis in *Eucalyptus grandis* canopies. *Oecologia* 88:494–503.

Leuning, R., Kelliher, F.M., de Pury, D.G.G. and Schulze, E.D. 1995. Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies. *Plant, Cell and Environment* 18:1183–1200.

LI-COR. 1990. LAI–2000 Plant Canopy Analyzer for rapid, non–destructive leaf area index measurements. LI–COR Inc., Nebraska, USA.

Linder, S. 1985. Potential and actual production in Australian forest stands. *In* Research for forest management. *Eds*. Landsberg, J.J. and Parsons, W., CSIRO, Melbourne, pp 11–35.

Linder, S., McMurtie, R.E. and Landsberg, J.J. 1985. Growth of eucalypts: a mathematical model applied to *Eucalyptus globulus*. *In* Crop physiology of forest trees. *Eds*. Tigerstedt, P.M.A., Puttonen, P. and Koski, V., University of Helsinki, Dept. of Plant Breeding, Helsinki, pp 117–126.

Long, J.N. and Smith, F.W. 1988. Leaf area – sapwood area relations of lodgepole pine as influenced by stand density and site index. *Canadian Journal of Forest Research* 18:247–250.

Long, J.N. and Smith, F.W. 1989. Estimating leaf area of *Abies lasiocarpa* across ranges of stand density and site quality. *Canadian Journal of Forest Research* 19:930–932.

Long, J.N. and Smith, F.W. 1990. Determinants of stemwood production in *Pinus contorta* var. latifolia forests: the influence of site quality and stand structure. *Journal of Applied Ecology* 27:847–856.

Lowther, J.R. 1980. Use of a single acid – hydrogen peroxide digest for the analysis of *Pinus radiata* needles. *Communications in Soil Science and Plant Analysis* 11:175–188.

Maguire, D.A. and Bennett, W.S. 1996. Patterns in vertical distribution of foliage in young coastal Douglas–fir. *Canadian Journal of Forest Research* 26:1991–2005.

Mäkelä, A. 1986. Implications of the pipe model theory on dry matter partitioning and height growth in trees. *Journal of Theoretical Biology* 123:103–120.

Mäkelä, A. and Vanninen, P. 1998. Impacts of size and competition on tree form and distribution of aboveground biomass in Scots pine. *Canadian Journal of Forest Research* 28:216–227.

Marshall, J.D. and Waring, R.H. 1986. Comparison of methods of estimating leaf area index in old–growth Douglas–fir. *Ecology* 67:975–979.

McKenzie, H. and Hawke, A. 1999. Growth response of *Eucalyptus regnans* dominant trees to thinning in New Zealand. *New Zealand Journal of Forestry Science* 29:301—310.

McMurtrie, R.E., Linder, S., Benson, M.L. and Wolf, L. 1986. A model of leaf area development for pine stands. *In* Crown and Canopy Structure in Relation to Productivity *Eds*. Fujimori, T. and Whitehead, D. Tsukuba, Japan, Forests and Forest Products Research Institute, pp 284–307.

McMurtrie, R.E., Landsberg, J.J. and Linder, S. 1989. Research priorities in field experiments on fast-growing tree plantations: implications of a mathmatical production model. *In* Biomass production by fast-growing trees. *Eds*. Pereira, J.S. and Landsberg, J.J., Kluwer Academic Publishers, pp 181—207.

McPherson, G. 1990. Statistics in Scientific Investigation. Its Basis, Applications and Interpretation. Springer–Verlag, London.

Medhurst, J.L., Battaglia, M., Cherry, M.L., Hunt, M.A., White, D.A. and Beadle, C.L. 1999. Allometric relationships for *Eucalyptus nitens* (Deane and Maiden) Maiden plantations. *Trees* 14:91–101.

Medlyn, B.E. 1996. Interactive effects of atmospheric carbon dioxide and leaf nitrogen concentration on canopy light use efficiency: a modelling analysis. *Tree Physiology* 16:201–209.

Mencuccini, M. and Grace, J. 1995. Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiology* 15:1–10.

Messina, M.G. 1992. Response of *Eucalyptus regnans* F. Muell. to thinning and urea fertilization in New Zealand. *Forest Ecology and Management* 51:269–283.

Misra, R.K., Turnbull, C.R.A., Cromer, R.N., Gibbons, A.K. and LaSala, A.V. 1998a. Below– and above–ground growth of *Eucalyptus nitens* in a young plantation. I. Biomass. *Forest Ecology and Management* 106:283–293.

Misra, R.K., Turnbull, C.R.A., Cromer, R.N., Gibbons, A.K., LaSala, A.V. and Ballard, L.M. 1998b. Below– and above–ground growth of *Eucalyptus nitens* in a young plantation II. Nitrogen and phosphorus. *Forest Ecology and Management* 106:295–306.

Mitchell, A.K., Barclay, H.J., Brix, H., Pollard, D.F.W., Benton, R. and deJong, R. 1996. Biomass and nutrient element dynamics in Douglas–fir: effects of thinning and nitrogen fertilization over 18 years. *Canadian Journal of Forest Research* 26:376–388.

Monteith, J.L. 1965. Evaporation and environment. *Symposium of the Society for Experimental Biology* 19:205—235.

Mooney, H.A., Ferrar, P.J. and Slatyer, R.O. 1978. Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. *Oecologia* 36:103–111.

Mori, S. and Hagihara, A. 1991. Crown profile of foliage area characterized with the Weibull distribution in a hinoki (*Chamaecyparis obtusa*) stand. *Trees* 5:149—152.

Morikawa, Y., Hattori, S. and Kiyono, Y. 1986. Transpiration of a 31–year–old

Chamaecyparis obtusa Endl. stand before and after thinning. *Tree Physiology* 2:105–114.

Mulligan, D.R. 1989. Leaf phosphorus and nitrogen concentration and net photosynthesis in *Eucalyptus* seedlings. *Tree Physiology* 5:149—157.

Nambiar, E.K.S., Squire, R.O., Sands, R. and Will, G.M. 1984. Manipulation of water and nutrients in plantations of fast growing species. *In* IUFRO symposium on site and productivity of fast growing plantations *Eds*. Grey, D.C., Schönau, A.P.G., Schutz, C.J. and van Laar, A. Pretoria and Pietermaritzburg, South Africa, South African Forest Research Institute, Pretoria, pp 489–506.

Neilsen, W.A. and Wilkinson, G.R. 1990. Eucalypt plantation silviculture: implications for sawlog production in Tasmania. *In* Prospects for Australian Forest Plantations. *Eds*. Dargavel, J. and Semple, N., Centre for Resource and Environmental Studies, Australian National University, Canberra, pp 209–223.

Neilsen, W.A. and Gerrand, A.M. 1999. Growth and branching habit of *Eucalyptus nitens* at different spacing and the effect on final crop selection. *Forest Ecology and Management* 123:217–229.

Niklas, K.J. 1992. Plant biomechanics: an engineering approach to plant form and function. University of Chicago Press, Chicago.

Nowak, J., Seiler, J.R., Cazell, B.H. and Kreh, R.E. 1990. Physiological differences in sun and shade foliage in thinned and unthinned loblolly pine. *In* Sixth biennial southern silvicultural research conference *Eds*. Coleman, S.S. and Neary, D.G. Memphis, Tennessee, Southeastern Forest Experiment Station, pp 541–548.

O'Grady, A.P., Eamus, D. and Hutley, L.B. 1999. Transpiration increases during the dry season: patterns of tree water use in eucalypt open–forests of northern

Australia. *Tree Physiology* 19:591–597.

Olbrich, B.W. 1991. The verification of the heat pulse velocity technique for estimating sap flow in *Eucalyptus grandis*. *Canadian Journal of Forest Research* 21:836–841.

Opie, J.E. 1976. Volume function for trees of all sizes, Forests Commission, Victoria, Technical Paper 25.

Oren, R., Phillips, N., Ewers, B.E., Pataki, D.E. and Megonigal, J.P. 1999. Sap–flux–scaled transpiration responses to light, vapour pressure deficit, and leaf area reduction in a flooded *Taxodium distichum* forest. *Tree Physiology* 19:337–347.

Pastor, J., Aber, J.D. and Melillo, J.M. 1984. Biomass prediction using generalized allometric regressions for some Northeast tree species. *Forest Ecology and Management* 7:265–274.

Pederick, L.A. 1979. Natural variation in shining gum (*Eucalyptus nitens*). *Australian Forest Research* 9:41—63.

Penner, M. and Deblonde, G. 1996. The relationship between leaf area and basal area growth in jack and red pine trees. *The Forestry Chronicle* 72:170–175.

Pereira, J.M.C., Tomé, M., Carreiras, J.M.B., Tomé, J.A., Pereira, J.S., David, J.S. and Fabião, A.M.D. 1997. Leaf area estimation from tree allometrics in *Eucalyptus globulus* plantations. *Canadian Journal of Forest Research* 27:166–173.

Pereira, J.S., Araújo, C.C. and Borralho, N. 1987. Crown structure of *Eucalyptus globulus* Labill. in a coppiced plantation. *In* Plant response to stress. *Ed.* Tenhunen, J.D., Springer–Verlag, Berlin, pp 521–53 0.

Pereira, J.S., Chaves, M.M., Carvalho, P.O., Caldeira, M.C. and Tomé, J. 1994. Carbon assimilation, growth and nitrogen supply in *Eucalyptus globulus* plants. *In* A whole plant perspective on carbon–nitrogen interactions. *Eds.* Roy, J. and Garnier, E., SPB Academic Publishing, The Hague, Netherlands, pp 79–89.

Peterson, J.A., Seiler, J.R., Nowak, J., Ginn, S.E. and Kreh, R.E. 1997. Growth and physiological responses of young loblolly pine stands to thinning. *Forest Science* 43:529–534.

Phillips, N., Oren, R. and Zimmermann, R. 1996. Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. *Plant Cell and Environment* 19:983—990.

Pinkard, E.A. 1997. Photosynthesis and resource allocation in the crowns of *Eucalyptus nitens* (Deane and Maiden) Maiden following green pruning. PhD thesis, University of Tasmania, 204 pp.

Pinkard, E.A. and Beadle, C.L. 1998a. Effects of green pruning on growth and stem shape of *Eucalyptus nitens* (Deane and Maiden) Maiden. *New Forests* 15:107–126.

Pinkard, E.A. and Beadle, C.L. 1998b. Aboveground biomass partitioning and crown architecture of *Eucalyptus nitens* following green pruning. *Canadian Journal of Forest Research* 28:1419–1428.

Pinkard, E.A., Beadle, C.L., Davidson, N.J. and Battaglia, M. 1998. Photosynthetic responses of *Eucalyptus nitens* (Deane and Maiden) Maiden to green pruning. *Trees* 12:119–129.

Pinkard, E.A., Battaglia, M., Beadle, C.L. and Sands, P.J. 1999. Modeling the effect

of physiological responses to green pruning on net biomass production of *Eucalyptus nitens*. *Tree Physiology* 19:1–12.

Pook, E.W. 1984. Canopy dynamics of *Eucalyptus maculata* Hook. I. Distribution and dynamics of leaf populations. *Australian Journal of Botany* 32:387–403.

Pothier, D., Margolis, H.A. and Waring, R.H. 1989. Patterns of change of saturated sapwood permeability and sapwood conductance with stand development. *Canadian Journal of Forest Research* 19:432–439.

Pothier, D. and Margolis, A. 1991. Analysis of growth and light interception of balsam fir and white birch saplings following precommercial thinning. *Annales des Sciences Forestieres* 48:123–132.

Pukkala, T., Miina, J. and Kellomäki, S. 1998. Response to different thinning intensities in young *Pinus sylvestris*. *Scandinavian Journal of Forest Research* 13:141–150.

Rauscher, H.M., Isebrands, J.G., Host, G.E., Dickson, R.E., Dickmann, D.I., Crow, T.R. and Michael, D.A. 1990. ECOPHYS: An ecophysiological growth process model for juvenile poplar. *Tree Physiology* 7:255–281.

Raven, P.H., Evert, R.F. and Eichhorn, S.E. 1986. Biology of Plants. 4th ed. Worth Publishers, New York.

Raymond, C.A., Owen, J.V. and Ravenwood, I.C. 1992. Genetic variation for frost tolerance in a breeding population of *Eucalyptus nitens*. *Silvae Genetica* 41:355–362.

Reed, D. and Tomé, M. 1998. Total aboveground biomass and net dry matter accumulation by plant component in young *Eucalyptus globulus* in response to irrigation. *Forest Ecology and Management* 103:21–32.

Reed, D.D., Mroz, G.D., Liechty, H.O., Jones, E.A., Cattelino, P.J., Balster, N.J. and Zhang, Y. 1995. Above– and below–ground biomass of precompetitive red pine in northern Michigan. *Canadian Journal of Forest Research* 25:1064–1069.

Robichaud, E. and Methven, I.R. 1992. The applicability of the pipe model theory for the prediction of foliage biomass in trees from natural, untreated black spruce stands. *Canadian Journal of Forest Research* 22:1118–1123.

Rogers, R. and Hinckley, T.M. 1979. Foliar weight and area related to current sapwood area in oak. *Forest Science* 25:298–303.

Rosati, A., Esparza, G., DeJong, T.M. and Pearcy, R.W. 1999. Influence of canopy light environment and nitrogen availability on leaf photosynthetic characteristics and photosynthetic nitrogen-use efficiency of field-grown nectarine trees. *Tree Physiology* 19:173—180.

Ryan, M.G. 1989. Sapwood volume for three subalpine conifers: predictive equations and ecological implications. *Canadian Journal of Forest Research* 19:1397–1401.

Ryan, M.G. 1990. Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. *Canadian Journal of Forest Research* 20:48—57.

Ryan, M.G., Gower, S.T., Hubbard, R.M., Waring, R.H., Gholz, H.L., Cropper Jr., W.P. and Running, S.W. 1995. Woody tissue maintenance respiration of four conifers in contrasting climates. *Oecologia* 101:133—140.

Ryan, M.G., Hubbard, R.M., Pongracic, S., Raison, R.J. and McMurtrie, R.E. 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiology* 16:333—343.

Ryan, M.G., Binkley, D. and Fownes, J.H. 1997. Age–related decline in forest productivity: pattern and process. *Advances in Ecological Research* 27:213–262.

Sands, P.J. 1995. Modelling canopy production. II. From single-leaf photosynthetic parameters to daily canopy photosynthesis. *Australian Journal of Plant Physiology* 22:603—614.

Sands, P.J. 1996. Modelling canopy production. III. Canopy light-utilisation efficiency and its sensitivity to physiological and environmental variables. *Australian Journal of Plant Physiology* 23:103—114.

Santantonio, D. 1989. Dry-matter partitioning and fine-root production in forests — new approaches to a difficult problem. *In* Biomass production by fast-growing trees. *Eds*. Pereira, J.S. and Landsberg, J.J., Kluwer Academic Publishers, pp 57—72.

SAS Institute Incorporated. 1990. SAS/STAT user's guide, version 6. SAS Institute Inc., Cary, NC.

Schoettle, A.W. and Smith, W.K. 1999. Interrelationships among light, photosynthesis and nitrogen in the crown of mature *Pinus contorta* ssp. *latifolia*. *Tree Physiology* 19:13–22.

Schönau, A.P.G. 1984. A factorial thinning experiment in *Eucalyptus grandis*. *Commonwealth Forestry Review* 63:285–295.

Schönau, A.P.G. and Coetzee, J. 1989. Initial spacing, stand density and thinning in eucalypt plantations. *Forest Ecology and Management* 29:245–266.

Shelburne, V.B., Hedden, R.L. and Allen, R.M. 1993. The effects of site, stand density, and sapwood permeability on the relationship between leaf area and

sapwood area in loblolly pine (*Pinus taeda* L.). *Forest Ecology and Management* 58:193–209.

Shelburne, V.B. and Hedden, R.L. 1996. Effect of stem height, dominance class, and site quality on sapwood permeability in loblolly pine, (*Pinus taeda* L.). *Forest Ecology and Management* 83:163–169.

Sheriff, D.W., Nambiar, E.K.S. and Fife, D.N. 1986. Relationships between nutrient status, carbon assimilation and water use efficiency in *Pinus radiata* (D. Don) needles. *Tree Physiology* 2:73—88.

Sheriff, D.W. and Nambiar, E.K.S. 1991. Nitrogen nutrition, growth and gas exchange in *Eucalyptus globulus* Labill. seedlings. *Australian Journal of Plant Physiology* 18:37–52.

Sheriff, D.W. 1992. Roles of carbon gain and allocation in growth at different nitrogen nutrition in *Eucalyptus camaldulensis* and *Eucalyptus globulus* seedlings. *Australian Journal of Plant Physiology* 19:637—652.

Sheriff, D.W. 1995. Gas exchange of field-grown *Pinus radiata* relationships with foliar nutrition and water potential, and with climatic variables. *Australian Journal of Plant Physiology* 22:1015—1026.

Sheriff, D.W., Margolis, H.A., Kaufmann, M.R. and Reich, P.B. 1995. Resource use efficiency. *In* Resource Physiology of Conifers: Aquisition, Allocation, and Utilization. *Eds*. Smith, W.K. and Hinckley, T.M., Academic Press, San Diego, pp 143—177.

Sheriff, D.W. and Mattay, J.P. 1995. Simultaneous effects of foliar nitrogen, temperature, and humidity on gas exchange in *Pinus radiata*. *Australian Journal of Plant Physiology* 22:615—626.

Sheriff, D.W. 1996. Responses of carbon gain and growth of *Pinus radiata* stands to thinning and fertilizing. *Tree Physiology* 16:527–536.

Shinozaki, K., Yoda, K., Hozumi, K. and Kira, T. 1964a. A quantitative analysis of plant form – the pipe model theory I. Basic analyses. *Japanese Journal of Ecology* 14:97–105.

Shinozaki, K., Yoda, K., Hozumi, K. and Kira, T. 1964b. A quantitative analysis of plant form – the pipe model theory II. Further evidence of the theory and its application in forest ecology. *Japanese Journal of Ecology* 14:133–139.

Siemon, G.R., Müller, W.J., Wood, G.B. and Forrest, W.G. 1980. Effect of thinning on the distribution and biomass of foliage in the crown of radiata pine. *New Zealand Journal of Forestry Science* 10:461–475.

Smethurst, P.J. 1998. Post-canopy-closure nutrient management in temperate eucalypt plantations: mini-review and research strategy. Technical Report No. 2. CRC for Sustainable Production Forestry, Hobart, Tasmania, 16 pp.

Smith, D.M. 1986. The practice of silviculture. 8th edition ed. John Wiley & Sons, New York.

Smith, F.W. and Long, J.N. 1989. The influence of canopy architecture on stemwood production and growth efficiency of *Pinus contorta* var. *latifolia*. *Journal of Applied Ecology* 26:681–691.

Snowdon, P. 1991. A ratio estimator for bias correction in logarithmic regressions. *Canadian Journal of Forest Research* 21:720–724.

Stackpole, D.J., Baker, T.G. and Duncan, M.J. 1999. Early growth trends following non–commercial thinning and pruning of three plantation eucalypts in northern Victoria. *In* Practising forestry today: the 18th biennial conference of the

Institute of Foresters of Australia *Eds*. Ellis, R.C. and Smethurst, P.J. Hobart, Australia, IFA Inc., pp 170–175.

Stephens, G.R. 1969. Productivity of red pine, 1. Foliage distribution in tree crown and stand canopy. *Agricultural Meteorology* 6:275–282.

Sutton, W.R. and Crowe, J.B. 1975. Selective pruning of radiata pine. *New Zealand Journal of Forestry Science* 5:171—195.

Swanson, R.H. and Whitfield, D.W.A. 1981. A numerical analysis of heat pulse velocity theory and practice. *Journal of Experimental Botany* 32:221—239.

Tang, Z., Chambers, J.L., Guddanti, S. and Barnett, J.P. 1999. Thinning, fertilization, and crown position interact to control physiological responses of loblolly pine. *Tree Physiology* 19:87–94.

Teklehaimanot, Z., Jarvis, P.G. and Ledger, D.C. 1991. Rainfall interception and boundary layer conductance in relation to tree spacing. *Journal of Hydrology* 123:261—278.

Teskey, R.O. and Sheriff, D.W. 1996. Water use by *Pinus radiata* trees in a plantation. *Tree Physiology* 16:273–279.

Turnbull, C.R.A., Beadle, C.L., Traill, J. and Richards, G. 1992. Benefits, problems and costs of excavators and bulldozers used for clearing operations in southern Tasmania. *Tasforests* 4:45–55.

Turnbull, C.R.A., Beadle, C.L., McLeod, R. and Cherry, M.L. 1997. Clearing with excavators and nitrogen fertilisers increases the yield of *Eucalyptus nitens* in plantations established on a native forest site in southern Tasmania. *Australian Forestry* 60:109–115.

Vertessy, R.A., Benyon, R.G., O'Sullivan, S.K. and Gribben, P.R. 1995. Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiology* 15:559–567.

Vertessy, R.A., Hatton, T.J., Reece, P., O'Sullivan, S.K. and Benyon, R.G. 1997. Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. *Tree Physiology* 17:747–756.

Vose, J.M. 1988. Patterns of leaf area distribution within crowns of nitrogen– and phosphorus–fertilized loblolly pine trees. *Forest Science* 34:564–573.

Walters, M.B. and Reich, P.B. 1989. Response of *Ulmus americana* seedlings to varying nitrogen and water status. 1. Photosynthesis and growth. *Tree Physiology* 5:159—172.

Wang, J.R., Simard, S.W. and Kimmins, J.P. 1995. Physiological responses of paper birch to thinning in British Columbia. *Forest Ecology and Management* 73:177–184.

Wang, Y.P. and Jarvis, P.G. 1990. Description and validation of an array model – MAESTRO. *Agricultural and Forest Meteorology* 51:257–280.

Waring, R.H., Gholz, H.L., Grier, C.C. and Plummer, M.L. 1976. Evaluating stem conducting tissue as an estimator of leaf area in four woody angiosperms. *Canadian Journal of Botany* 55:1474–1477.

Waring, R.H., Schroeder, P.E. and Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. *Canadian Journal of Forest Research* 12:556–560.

Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. *Advances in Ecological Research* 13:327–354.

Webb, A.W. 1966. The effect of thinning of mountain ash (*Eucalyptus regnans*) in Victoria. PhD thesis, University of Melbourne

Webb, A.W. and Incoll, W.D. 1969. Thinning ash–type eucalypts. Forest Commission, Victoria, 13–14 pp.

West, P.W. 1979. Estimation of height, bark thickness and plot volume in regrowth eucalypt forest. *Australian Journal of Forest Research* 9:295–308.

West, P.W., Jackett, D.R. and Sykes, S.J. 1989. Stresses in, and the shape of, tree stems in forest monoculture. *Journal of Theoretical Biology* 140:327–343.

West, P.W. 1993. Model of above–ground assimilate partitioning and growth of individual trees in even–aged forest monoculture. *Journal of Theoretical Biology* 161:369–394.

White, D., Beadle, C., Worledge, D., Honeysett, J. and Cherry, M. 1998. The influence of drought on the relationship between leaf and conducting sapwood area in *Eucalyptus globulus* and *Eucalyptus nitens*. *Trees* 12:406–414.

White, D.A. 1996. Physiological responses to drought of *Eucalyptus globulus* and *E. nitens* in plantations. PhD thesis, University of Tasmania, 166 pp.

White, D.A., Beadle, C.L., Sands, P.J., Worledge, D. and Honeysett, J.L. 1999a. Quantifying the effect of cumulative water stress on stomatal conductance of *Eucalyptus globulus* and *Eucalyptus nitens*: a phenomenological approach. *Australian Journal of Plant Physiology* 26:17–27.

White, D.A., Beadle, C.L. and Worledge, D. 1999b. Control of transpiration in an irrigated *Eucalyptus globulus* Labill. plantation. *Plant, Cell and Environment* 23:123—134.

Whitehead, D. 1978. The estimation of foliage area from sapwood basal area in Scots pine. *Forestry* 51:137–149.

Whitehead, D., Edwards, W.R.N. and Jarvis, P.G. 1984a. Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. *Canadian Journal of Forest Research* 14:940–947.

Whitehead, D., Jarvis, P.G. and Waring, R.H. 1984b. Stomatal conductance, transpiration and resistance to water uptake in a *Pinus sylvestris* spacing experiment. *Canadian Journal of Forest Research* 14:692–700.

Whitehead, D. 1986. Dry matter production and transpiration by *Pinus radiata* in relation to canopy architecture. *In* Crown and Canopy Structure in Relation to Productivity *Eds*. Fujimori, T. and Whitehead, D. Tsukuba, Japan, Forestry and Forest Products Research Institute, pp 243–262.

Whitehead, D., Grace, J.C. and Godfrey, M.J.S. 1990. Architectural distribution of foliage in individual *Pinus radiata* D. Don crowns and the effects of clumping on radiation interception. *Tree Physiology* 7:135–155.

Whitford, K.R., Colquhoun, I.J., Lang, A.R.G. and Harper, B.M. 1995. Measuring leaf area index in a sparse eucalypt forest: a comparison of estimates from direct measurement, hemispherical photography, sunlight transmittance and allometric regression. *Agricultural and Forest Meteorology* 74:237–249.

Whyte, A.G.D. and Woollons, R.C. 1990. Modelling stand growth of radiata pine thinned to varying densities. *Canadian Journal of Forest Research* 20:1069–1076.

Williamson, M.J. 1979. Growth of *Eucalyptus saligna* in a thinning trial at Waipoua. *New Zealand Journal of Forestry* 26:245–250.

Wilson, K.B., Baldocchi, D.D. and Hanson, P.J. 2000. Spatial and seasonal variability of photosynthetic parameters and their relationship to leaf nitrogen in a deciduous forest. *Tree Physiology* 20:565—578.

Wullschleger, S.D. and King, A.W. 2000. Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees. *Tree Physiology* 20:511—518.

Xu, M. and Harrington, T.B. 1998. Foliage biomass distribution of loblolly pine as affected by tree dominance, crown size, and stand characteristics. *Canadian Journal of Forest Research* 28:887–892.

Yang, J.L. and Waugh, G. 1996. Potential of plantation–grown eucalypts for structural sawn products. II. *Eucalyptus nitens* (Dean & Maiden) Maiden and *E. regnans* F. Muell. *Australian Forestry* 59:99–107.

Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W. and Kaufmann, M.R. 1994. Evidence of reduced photosynthetic rates in old trees. *Forest Science* 40:513–527.

Zang, D., Beadle, C.L. and White, D.A. 1996. Variation of sapflow velocity in *Eucalyptus globulus* with position in sapwood and use of a correction coefficient. *Tree Physiology* 16:697–703.

Zimmerman, M.H. 1983. Xylem structure and the ascent of sap. Springer–Verlag, New York.

Zotz, G., Tyree, M.T., Patiño, S. and Carlton, M.R. 1998. Hydraulic architecture and water use of selected species from a lower montane forest in Panama. *Trees* 12:302–309.